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FOUR SPECIES OF *HYMENOLEPIS* WEINL. PARASITIC IN THE OYSTERCATCHER, *HAEMATOPUS OSTRALEGUS* LINN.

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(With 18 Figures in the Text)

INTRODUCTION

THE material for the present investigation was obtained from nine oystercatchers shot on the coast of Cardigan and one shot at Peterstone on the coast of Monmouth; for the material from the latter bird the writer is indebted to Mr Thomas Walker, M.Sc., of University College, Cardiff.

Hymenolepis clandestina (Krabbe, 1869) and *H. rectacantha* Fuhrmann, 1906, were recovered from birds shot on the salt marshes of the Dovey Estuary in Cardigan and of Peterstone in Monmouth; *H. lauriei* n.sp. was also recovered from two birds taken on the Dovey mud-flats. *H. cambrensis* n.sp. occurred twice in birds shot on the rocky parts of the Cardigan coast, at Monk's Cave south of Aberystwyth, and Wallog south of Borth. The data are too scanty, however, to suggest a correlation between the species of parasite and the type of feeding-ground frequented by the host.

MORPHOLOGY OF SPECIES

(1) **Hymenolepis clandestina** (Krabbe, 1869) (Figs. 1–5)

Syn. *Taenia clandestina* Krabbe, 1869.
Hymenolepis (*Drepanidotaenia*) *clandestina* Cohn, 1904.

Creplin's collection included a tube (No. 26, EEg) of cestodes labelled *Taenia clandestina*, from an oystercatcher, *Haematopus ostralegus*; Greifswald, June. Krabbe (1869) gave a morphological description of Creplin's material, whilst Cohn (1904) gave an account of its anatomy as far as the poor state of preservation of the original material would allow. The specimens at the writer's disposal, containing the hitherto unobserved gravid condition, provide opportunity for a further definition of the characters of this species.

DESCRIPTION. The maximum length of strobila is 100 mm. (Krabbe, 70 mm.; Cohn, 35 mm.), whilst its breadth reaches 1·4 mm. The scolex (Fig. 1) is subspherical in shape, with a diameter of 320μ. The rostellum in all the specimens is retracted, and bears 10 hooks of length 51–55μ (Krabbe, 47μ;

Cohn, 40μ). The shape of the rostellar hook (Fig. 2) agrees closely with the drawing by Krabbe (1869, pl. 8, fig. 209) and also with that of Cohn (1904, fig. 9). It is a robust type with well-marked dorsal and ventral roots, the shape remaining constant within close limits of variation. The extended rostellum was not observed either by Krabbe or Cohn, but the latter suggested that it might be of considerable length on account of the size of the rostellar sac; this sac measures 260μ, and reaches well beyond the posterior borders of the suckers. The region between the outer and inner sacs is occupied by a mass of deep-staining glandular tissue. The suckers are small and muscular, 110μ in diameter, and are directed antero-laterally when the rostellum is completely retracted.

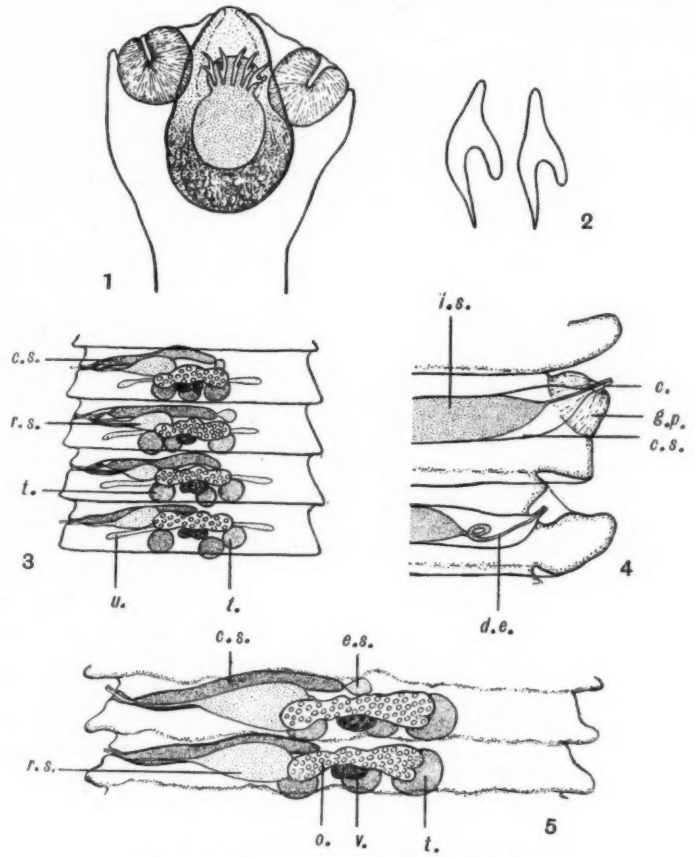
The neck is long and thin, 2 × 0·18 mm., and is followed by a long immature region showing very indistinct segmentation.

The onset of maturity in the strobila is very retarded, a fact which was noticed by Cohn, and which caused him to predict that the gravid cestode must be of great length. Of especial interest also is the relation between the age of the individual tapeworm and the size and shape of its proglottids. In young strobilae, which although gravid are still complete, the mature proglottids measure 0·13 mm. long by 0·73 mm. broad; in older specimens the length is but 0·1 mm. whilst the breadth is 1 mm., showing a decrease in the length-breadth ratio of mature proglottids from approximately 1 : 5½ to 1 : 10 with progressing age. This difference between young and old strobilae as regards the proportions of their segments is accompanied by apparent differences in the disposition of the genitalia, so that the testes become linear, occupying the whole length of the segments in older strobilae, whilst in young worms they have a greater latitude of disposition (Figs. 3, 5). A parallel change of length-breadth ratio occurs in gravid proglottids, typical measurements for a gravid segment in a complete worm being 0·27 × 0·77 mm., and in an incomplete worm 0·11 × 1·2 mm., showing a decrease of length-breadth ratio from 1 : 3 to 1 : 11. The posterior margins of the mature and gravid proglottids show a wavy outline in old strobilae (Fig. 5), whilst in young worms the margins are linear (Fig. 3).

The large ventral excretory vessels are 43μ in diameter; dorsal and transverse vessels were not observed.

The three testes, which lie dorsal in the parenchyma, are arranged at the posterior end of the proglottis, generally one on the poral side and two on the aporal side of the female genitalia. As was found by Cohn (1904), however, some segments are exceptional in having two on the poral side and one on the aporal, whilst still others have a middle testis medianly situated (Fig. 3). In the younger strobilae whose mature segments are relatively long, irregularities may occur in the anteroposterior relation of the testes. Thus the middle testis may be obliquely behind the aporal testis, as in *H. gracilis*, or directly behind it, as in *H. liguloides*, or obliquely in front of it, as in *H. coronula*. In older specimens, however, the testes are almost always in the same transverse line,

occupying the greater part of the length of the segment. The mature testes are generally oval in shape, typical measurements being 85 μ long by 106 μ broad. In older segments the "spent" testes become more rounded in shape and



Figs. 1–5. *Hymenolepis clandestina* (Krabbe, 1869).

Fig. 1. Scolex, 320 μ in diameter. Fig. 2. Rostellar hooks, 10, 51–55 μ long. Fig. 3. Mature proglottids of young complete strobila, 0·73 mm. broad; ventral view. Fig. 4. Poral margins of mature segments, showing prominent genital papilla. Fig. 5. Mature proglottids of older incomplete strobila, 1 mm. broad; ventral view. For lettering see p. 412.

attain a size of 130 × 150 μ. The cirrus-sac is well developed, slightly overreaching the median line in proglottids of young worms (Fig. 3), becoming relatively shorter in the broad proglottids of older strobilae, where it rarely reaches the median line (Fig. 5). Its measurements are typically 410 × 45 μ when relaxed, contracting to a length of 320 μ with the eversion of the cirrus. Situated dorsally in the parenchyma, it extends transversely across the anterior

poral half of the segment, curving posteriorly to open into the genital pore at the middle of the proglottidal margin. Both cirrus-sac and vagina pass outwards dorsally to the excretory vessels. A small external vesicula seminalis was observed in some preparations situated immediately outside the aporal tip of the cirrus-sac, and directly anterior to the aporal wing of the ovary. A large internal vesicula seminalis is always present, occupying almost the whole of the cirrus-sac. A fine ductus ejaculatorius of variable length connects the internal vesicula seminalis with the marginal genital atrium (Fig. 4); in some instances the ductus is long and coiled, traversing the whole length of the cirrus-sac.

The genital pores are strictly unilateral on the right side, and the wide genital atrium is capable of being everted to form a prominent genital papilla (Fig. 4). The everted cirrus is short and slender, measuring $43 \times 8 \mu$.

The vagina expands into a large receptaculum seminis extending from the poral water vessels almost to the median line. It is variable in size, typical measurements being $85 \times 128 \mu$ in one segment and $96 \times 246 \mu$ in another. In segments approaching the gravid condition the receptaculum seminis is distended with sperm and assumes a spherical outline, with a diameter of about 170μ. The ovary is transversely elongate, showing slight but distinct lobing. In younger strobilae its breadth is 234μ, whilst in the broad proglottids of older worms it measures up to 362μ. The vitellarium is compact and situated medianly, dorsal to the ovarian commissure; its breadth averages 95μ.

The uterus arises as a transverse sac readily discernible in mature proglottids (Fig. 3). With the onset of the gravid condition, the right and left halves of the transverse uterus become distended with eggs, the uterine organ assuming a distinctly bisaccate appearance. Each sac may in turn become more or less deeply lobed. In the older, fully gravid segments, the uterus appears as a spacious sac, filled with eggs each with a diameter of 47μ.

In young strobilae it was often observed that only about 10% of the proglottids in the gravid region contained a fully developed uterus with ripe eggs. In the remaining 90% of the segments the uterine sac remained rudimentary, this condition being invariably associated with an empty receptaculum seminis. The cause of this lack of insemination with its attendant infertility in young worms is obscure; in the older incomplete strobilae with broad segments, the uterus is invariably normally developed and full of eggs, a condition associated with a distended receptaculum seminis.

(2) **Hymenolepis cambrensis** n.sp. (Figs. 6–10)

Description. *Hymenolepis cambrensis* n.sp. is a small worm, the length of the strobila being 4·5 mm.; its breadth increases gradually to the posterior end where it reaches 0·46 mm. The scolex (Fig. 6) is triangular in shape, measuring $150–210 \mu$ in diameter at the base, and tapering gradually towards the apex. The rostellum, when extended, attains a length of 220μ and a diameter of 20μ.

The rostellar hooks are 10 in number and 53 μ in length, with a long dorsal and a very short ventral root, the latter being much shorter than the blade (Fig. 7). A characteristic feature of the rostellar hook is that the ventral root is directed backwards, forming an acute angle with the dorsal root, and appearing continuous with the blade. The outer rostellar sac has a diameter of 64 μ and extends backwards a little beyond the posterior borders of the suckers. The inner rostellar sac appears as a narrow tube entirely confined to the rostellum when the latter is extended (Fig. 6). The suckers are slightly oval, typical measurements being $96 \times 85\,\mu$; their musculature is not well developed.

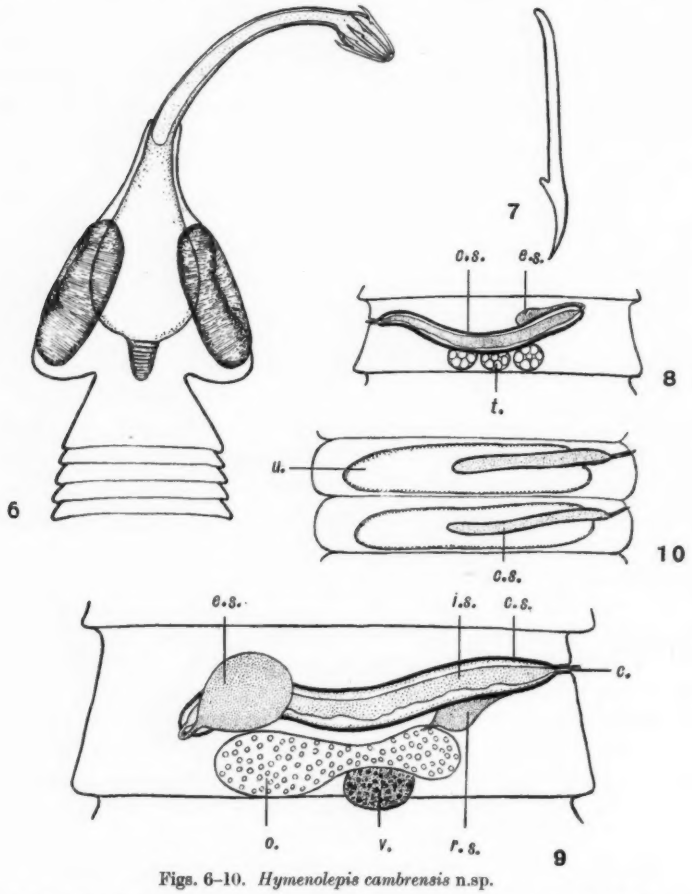
The neck is very short, 0·064–0·074 mm. in length, its breadth varying from 0·064 to 0·096 mm. according to the state of contraction of the material. The neck widens abruptly from its insertion into the scolex to the immature region of the strobila.

The segmented strobila consists generally of some 100 segments, of which the first 15 or so are immature, the vast majority are mature, whilst the last 12–15 are gravid. The immature segments are distinct, short and broad, measuring $0{\cdot}011 \times 0{\cdot}117$ mm. The mature proglottids measure $0{\cdot}064 \times 0{\cdot}220$ mm. in younger specimens, their length-breadth ratio being 1 : 3½ as contrasted with 1 : 5 in the mature segments of older strobilae. The gravid segments are relatively large, measuring 0·107 mm. long by 0·450 mm. broad; the last two or three proglottids possess rounded corners, the intersegmental fissures extending gradually inwards to the point of detachment of the segments.

The male genitalia develop well before the female. Rudiments of the testes appear in the 15–20th segments behind the scolex; they reach maturity in the subsequent 4–6 segments, remaining in this state for a length of some 20 segments, when they are already beginning to disintegrate, and the female glands are becoming apparent as large organs occupying the ventral parenchyma. It would seem therefore that in *H. cambrensis* n.sp. we have a condition of complete protandry, the male glands being entirely "spent" before the female genitalia are yet developed. This segregation of the sexes along the length of the strobila increases the capacity for autofecundation, since it enables the massive external and internal vesiculae seminales to store large quantities of sperm in readiness for the period of female activity. In some strobilae even the receptaculum seminis was observed to contain quantities of sperm before the onset of female activity, the process of oogenesis commencing only after autoinsemination had already been ensured.

The three testes, confined to the extreme anterior part of the mature strobila, are often extremely difficult to distinguish. Disposed in a transverse line at the posterior border of the proglottis (Fig. 8), they are spherical in shape, with a diameter of 19 μ. They are situated dorsally in the parenchyma, being dorsal to and partly overlying the cirrus-sac. The vas deferens expands into a large external vesicula seminalis which usually overlies the aporal tip of the cirrus-sac (Figs. 8, 9); in some segments it attains a diameter of 30 μ. The well-developed cirrus-sac, measuring $160 \times 16\,\mu$, extends well beyond the median

line up to the probable position of the aporal water vessels. It is dorsal to the vagina, but curves ventrally during its course so as to become ventral to both the testes and external vesicula seminalis; it also frequently curves posteriorly so as to approach the posterior border of the proglottis and lie directly under



Figs. 6–10. *Hymenolepis cambrensis* n.sp.

Fig. 6. Scolex, 150–210 μ broad. Fig. 7. Rostellar hook, 10, 53 μ long. Fig. 8. "Mature male" proglottis, 0·220 mm. broad; ventral view. Fig. 9 "Mature female" proglottis; dorsal view. Fig. 10. Gravid segments; dorsal view. For lettering see p. 412.

the testes. The cirrus-sac is occupied by a long internal vesicula seminalis narrowing into the cirrus at the marginal genital pore (Figs. 8–10).

The genital pores are unilateral on the right side, each pore being situated in the anterior third of the proglottidal margin. The genital atrium is narrow and deep, and the everted cirrus, measuring 17 × 1·5 μ, seldom extends beyond

the cavity of the atrium. The rudimentary cirrus, like the condition of complete protandry and the regular fertility of the gravid segments, points to autofecundation as being the constant mode of reproduction in *H. cambrensis* n.sp.

The ovary is distinctly bilobed, both lobes being usually long and oval, and the left lobe being generally larger than the right; the two lobes are connected by a broad isthmus (Fig. 9). The vitellarium is compact and oval, typical measurements being 17 μ long by 30 μ broad. It is ventral to the ovary, generally to the right of the median line, partly underlying the ovarian isthmus, and also partly underlying the small right ovarian wing. Its displacement to the right is more marked in some segments than in others. The shell gland can sometimes be observed as a dark-staining mass dorsal to the ovarian isthmus. The vagina distends to form a receptaculum seminis immediately inside the probable position of the poral excretory vessels (Fig. 9).

The uterus is a simple sac, occupying almost the whole of the gravid segment. It is traversed dorsally by the cirrus-sac, which is the only other genital structure retained in the gravid segments (Fig. 10).

Hymenolepis cambrensis n.sp.

SPECIFIC DIAGNOSIS. *Hymenolepis* Weinland, 1858; with generic characters. Length 4·5 mm., maximum breadth 0·46 mm. Scolex 150–210 μ broad. Rostellum 220 × 20 μ, bearing 10 hooks, 53 μ long, with very short, backwardly pointing ventral roots. Rostellar sac 64 μ in diameter, extending beyond posterior borders of suckers. Suckers 96 × 85 μ, with weak musculature. Neck short, 0·064–0·074 mm. long × 0·064–0·096 mm. broad. Strobila of about 100 segments, showing complete protandry. Length-breadth ratio of mature proglottids 1 : 3½ to 1 : 5, typical measurements being 0·064 × 0·220 mm. Testes 19 μ in diameter, disposed in a transverse line at posterior border of proglottis. External vesicula seminalis 30 μ in diameter, overlying aporal tip of cirrus-sac. Cirrus-sac 160 × 16 μ extending probably to aporal water vessels, and containing extensive internal vesicula seminalis. Cirrus rudimentary, 17 × 1·5 μ. Ovary bilobed with broad isthmus. Vitellarium 17 × 30 μ, ventral to the ovary, right of the median line. Receptaculum seminis present immediately inside probable position of poral excretory vessels. Uterus a large oval sac.

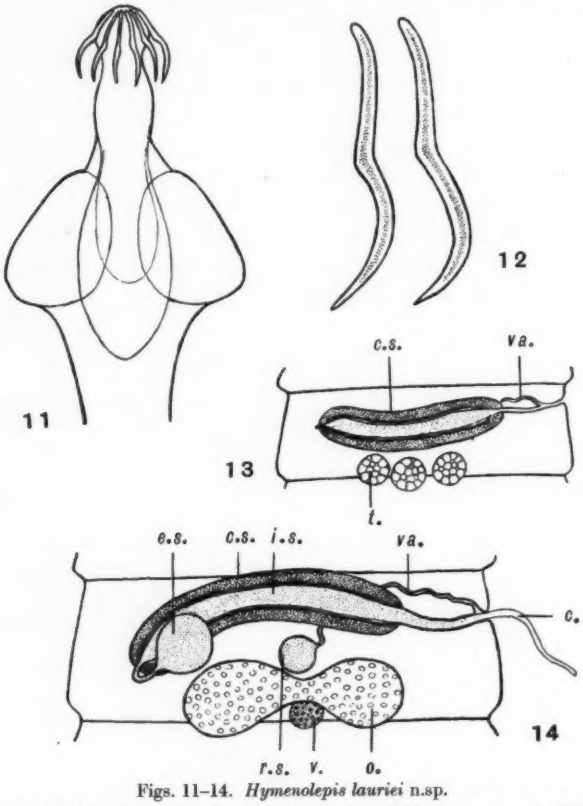
Habitat. Small intestine of *Haematopus ostralegus*.

Locality and dates. Monk's Cave, Cardigan coast, July 1933, December 1935; Wallog, Cardigan coast, June 1934.

(3) **Hymenolepis lauriei** n.sp. (Figs. 11–14)

DESCRIPTION. The strobila of *H. lauriei* n.sp. is small, with a length of 3·37 mm. and a maximum breadth of 0·3 mm. The scolex (Fig. 11) is well developed, 266 μ in diameter, bearing a robust, prominent rostellum of length 170 μ and breadth 53 μ; the rostellar tip is generally slightly swollen. The 10 rostellar hooks are 86–96 μ long, the average measurement being 94 μ. They are similar in shape (Fig. 12) to the hooks of *Hymenolepis nitida* (Krabbe, 1869), *H. nitidulans* (Krabbe, 1882), and *H. charadrii* Yamaguti, 1935, their characteristic feature being the absence of a ventral root. The dorsal root is long, its length being approximately equal to that of the blade. The blade is

curved and tapers gradually to a fine point at its tip; the curvature of the hook becomes more pronounced when the rostellum is retracted, the minimal length of 86 μ being generally associated with the retracted rostellum. The outer rostellar sac (Fig. 11) is 234 μ long by 75 μ broad, and reaches well beyond the posterior borders of the suckers. The suckers are variable in shape, generally



Figs. 11–14. *Hymenolepis lauriei* n.sp.

Fig. 11. Scolex, 266 μ broad. Fig. 12. Rostellar hooks, 10, 86–96 μ long. Fig. 13. "Mature male" proglottis; dorsal view. Fig. 14. "Mature female" proglottis, 0·213 mm. broad; dorsal view. For lettering see p. 412.

slightly oval, measuring 128 × 117 μ. The scolex merges into the segmented strobila without an intervening neck.

The strobila consists of 30–40 segments, of which the first 15–20 are immature, the subsequent 7–10 segments contain only male genitalia (Fig. 13), and the remainder contain both male and female glands, the testes gradually disappearing towards the posterior end of the strobila (Fig. 14). The gravid condition was not observed. The immature segments are distinct, with salient posterior borders; the mature segments retain a length-breadth ratio of 1 : 2½,

typical measurements being 0·085 × 0·213 mm. Excretory vessels were not discernible in whole mounts.

The three spherical testes (Fig. 13), 32 μ in diameter, are arranged in a transverse row across the posterior border of the proglottis; in the anterior segments the rudiments of the testes may be arranged in a slightly different manner, generally with the middle testis partly posterior to the other two. The spherical external vesicula seminalis (Fig. 14) is directly dorsal to the aporal tip of the cirrus-sac, with a diameter of 38 μ. The cirrus-sac, 150 × 34 μ, has an extremely muscular wall, whose thickness reaches 10·6 μ. This abnormally strong musculature, however, extends from the aporal tip of the cirrus sac only to within 32–38 μ from the genital atrium; the distal portion of the sac is provided with a thin, non-muscular wall (Fig. 14). The internal vesicula seminalis occupies the whole of the cavity of the cirrus-sac. The genital atrium is narrow and fairly deep, opening by a genital pore in the anterior third of the proglottidal margin; the pores are unilateral on the right side of the strobila. The everted cirrus is long, slender, and unarmed, measuring 85 × 7·4 μ.

The transversely elongate ovary measures 117 μ in transverse diameter; it is distinctly two winged, the left wing being generally larger than the right. The small rounded vitellarium, 32 μ in diameter, is situated medianly, ventral to the ovarian isthmus. The vagina passes inwards from the genital atrium as an undulating tube, at first anterior to the cirrus-sac, but later curving under it to enter a spherical receptaculum seminis in the region of the ootype. The receptaculum (Fig. 14), 21 μ in diameter, is median in position, immediately anterior and dorsal to the ovarian isthmus. The uterus and eggs were not observed.

DISCUSSION. *Hymenolepis lauriei* n.sp. stands close to *H. charadrii* Yamaguti, 1935, a species recorded from *Charadrius alexandrinus dealbatus* in Japan. The writer was fortunate in obtaining specimens of *H. charadrii* from a ringed-plover, *Aegialitis hiaticola*, shot on the Dovey mud-flats in the locality where oystercatchers were found to be parasitized by *H. lauriei* n.sp. A comparison of the characters of the two cestodes proves beyond doubt that they are distinct species, the chief distinguishing features being the length of the rostellar hooks (*H. lauriei*, 86–96 μ; *H. charadrii*, 57–66 μ), the size and shape of the cirrus-sac (*H. lauriei*, 150 × 34 μ, with a cylindrical muscular part traversing the whole median field of the proglottis; *H. charadrii*, 90 × 30–36 μ, spindle-shaped, muscular, scarcely reaching the median line of the proglottis), and the size of the testes (*H. lauriei*, 32 μ; *H. charadrii*, 20–24 μ). Other differences are apparent in the size of the scolex and suckers, and in the shape of the vas deferens, which is recurved dorsally in *H. lauriei* n.sp. and straight in *H. charadrii* Yamaguti, 1935.

Hymenolepis lauriei n.sp.

SPECIFIC DIAGNOSIS. *Hymenolepis* Weinland, 1858; with generic characters. Length 3·37 mm., maximum breadth 0·3 mm. Scolex 266 μ broad. Rostellum 170 × 53 μ, bearing 10 hooks, 86–96 μ long, averaging 94 μ. Outer rostellar sac 234 × 75 μ, extending well beyond posterior borders of suckers. Suckers generally oval, 128 × 117 μ. Neck absent. Strobila of

30–40 segments; typical mature proglottis 0·085 × 0·213 mm., with length-breadth ratio of 1 : 2½. Testes spherical, 32 μ in diameter, arranged in transverse row at posterior border of proglottis. External vesicula seminalis spherical, 38 μ in diameter, overlying aporal tip of cirrus-sac. Cirrus-sac 150 × 34 μ, its aporal part with muscular wall, 10·6 μ thick, traversing whole median field of proglottis. Cirrus long, slender, unarmed, 85 × 7·4 μ. Ovary transversely elongate with diameter of 117 μ, distinctly two-winged. Vitellarium rounded, 32 μ in diameter. Receptaculum seminis spherical, 21 μ in diameter, median, anterior to ovarian isthmus. Uterus and eggs not observed.

Habitat. Small intestine of *Haematopus ostralegus*.
Locality and date. Dovey mud-flats, Cardigan coast, February 1935.

(4) **Hymenolepis rectacantha** Fuhrmann, 1906 (Figs. 15–18)

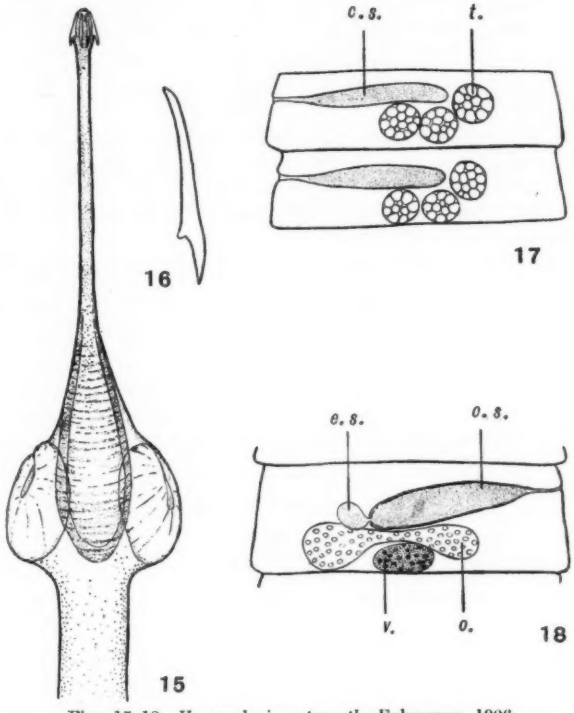
The original material of this species was collected from *Aegialitis hiaticola* and stored in Tube 38 at the Stuttgart Museum. Fuhrmann (1906) based his specific diagnosis on the morphology of the scolex and male genitalia, the available specimens being too immature to reveal the morphology of the female reproductive structures. As far as the present writer is aware there is no further record of *Hymenolepis rectacantha* Fuhrmann, 1906.

Description. The strobila of *H. rectacantha* Fuhrmann, 1906, measures 35 mm. in length and 0·32 mm. in breadth; it is slender, thin, and extremely fragile, twisting very readily during the process of mounting. The scolex, 150–170 μ in diameter, bears a long, slender rostellum, measuring 455 × 21 μ (Fig. 15). The rostellar tip is generally slightly swollen, with a diameter reaching 32 μ. The 10 rostellar hooks are 43 μ long, their shape (Fig. 16) similar to that figured by Fuhrmann (1906, fig. 27). The outer rostellar sac measures 170 μ long by 74 μ broad, and extends to the level of the posterior borders of the suckers. The suckers measure 85 × 75 μ, with weakly developed musculature.

The neck is long and slender, 1 × 0·045 mm., merging insensibly into the immature region of the segmented strobila. The segments of the latter region are at first indistinct, without salient posterior borders. The mature proglottids measure 0·064 mm. long by 0·213 mm. broad, whilst gravid segments typically measure 0·055 mm. long by 0·30 mm. broad.

The three testes are spherical, with a diameter of 21–23 μ, arranged as in *H. gracilis*, with the aporal testis obliquely in front of the middle testis (Fig. 17). In some proglottids the aporal testis is directly in front of the middle testis, as in *H. liguloides*. On no occasion in the present work were the testes observed to lie in a transverse line as described by Fuhrmann (1906). The cirrus-sac extends to the median line or beyond; its wall is thin, becoming appreciably distended with the accumulation of sperm in the internal vesicula seminalis (Fig. 18). Its measurements are 70 × 15 μ. A very small external vesicula seminalis is sometimes discernible immediately outside the aporal tip of the cirrus-sac. The everted condition of the cirrus was not observed; the genital atrium is narrow and deep, invariably opening on the right side of the segment.

The ovary is transversely elongate, with the two wings connected by a fairly narrow isthmus. Its transverse diameter is 75 μ. The vitellarium is large and oval, with a transverse diameter of 34 μ. The uterus is saccular, occupying practically the whole of the gravid proglottis. Ripe eggs were not observed.



Figs. 15–18. *Hymenolepis rectacantha* Fuhrmann, 1906.

Fig. 15. Scolex, 150–170 μ broad. Fig. 16. Rostellar hook, 10, 43 μ long. Fig. 17. Mature proglottids showing male genitalia; ventral view. Fig. 18. Mature proglottis showing female genitalia, 0·213 mm. broad; dorsal view. For lettering see p. 412.

ACKNOWLEDGEMENTS

One of the species described in the present paper is named in honour of Prof. R. D. Laurie, to whom the writer is deeply indebted for unfailing encouragement during the course of his work at Aberystwyth. Also to Dr Gwendolen Rees sincere gratitude is due for expert guidance and helpful advice.

Lettering for Figures

c.	cirrus	*o.*	ovary.
c.s.	cirrus-sac.	*r.s.*	receptaculum seminis.
d.e.	ductus ejaculatorius.	*t.*	testis.
e.s.	external vesicula seminalis.	*u.*	uterus.
g.p.	genital papilla.	*v.*	vitellarium.
i.s.	internal vesicula seminalis.	*va.*	vagina.

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ON A NEW GENUS AND SPECIES OF RHADINORHYNCHIDAE (ACANTHOCEPHALA)[1]

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(With Plate XII)

In the vicinity of Grand Isle, Louisiana, *Menticirrhus americanus*, a marine fish of the surmullet family, carries in the intestine an acanthocephalan which has been previously undescribed. The attention of the writers was first called to this species by collections made available by Mr J. E. Tobie. Additional specimens were later secured from Dr H. J. Bennett. This new species is clearly a representative of the family Rhadinorhynchidae but in it are embodied peculiarities and combinations of characters which preclude its inclusion in any previously recognized genus. Hence a new genus is herein proposed and the species is described as *Illiosentis furcatus*.

Illiosentis n.g.

Rhadinorhynchidae, in which the posterior extremity of the female is modified into dorso-posterior and ventro-posterior protuberances, the dorsal of which bears the genital opening. Situated in the body wall in a cleft between the protuberances is a fan-shaped muscular organ. Posterior extremity of body bearing cuticular spines in the female only. Anterior body spines present in both sexes. Proboscis relatively long, with a heavy investing cuticular covering. A circle of hooks at proboscis base, in alignment with the longitudinal rows on the remainder of the proboscis, but with the ventral hooks of this basal circle greatly enlarged. Lemnisci about one and one-half times as long as receptacle. Eight cement glands elongate, pyriform to clavate. Testes broadly contiguous. Brain within anterior extremity of the receptacle at base of proboscis.

Genotype: *Illiosentis furcatus* n.g., n.sp.

Illiosentis differs from all other genera of the Rhadinorhynchidae, except *Telosentis*, in the possession of cuticular spines on the genital extremity. In *Telosentis*, scattered spines occur on the genital extremity of both sexes, but in *Illiosentis* spines are restricted to the female and occur in fairly definite pattern around the genital pore and on the ventro-posterior protuberance.

[1] Contributions from the Zoological Laboratory of the University of Illinois, No. 530, and from the Parasitology Laboratory, Department of Tropical Medicine, Tulane University of Louisiana.

The conspicuous investing cuticula over the surface of the proboscis is common to both *Tegorhynchus* and *Illiosentis*. The latter is readily distinguished from the former by the greatly enlarged ventral hooks in the basal circle of proboscis hooks. These large basal hooks in *Illiosentis* are modifications of a portion of the basal circle and therein differ from the isolated ventral crescent of basal hooks characteristic of *Rhadinorhynchus tenuicornis* as also from the unspecialized basal circle of hooks found in *Tegorhynchus* and in *Telosentis*.

Illiosentis furcatus n.sp.
(Figs. 1–4)

Characters of the genus Illiosentis. Body elongate, cylindrical, females 5·6–21·5 mm. long and 0·35–0·62 mm. in maximum diameter; males 4–9·8 mm. long and 0·32–0·52 mm. in diameter. Posterior extremity of females (Pl. XII, fig. 4) peculiarly modified into dorso-posterior and ventro-posterior protuberances of which the former bears the vaginal orifice. Within the body, in a cleft between the two protuberances, is a double, fan-shaped, muscular organ (Pl. XII, fig. 4). Body spines are restricted to a single anterior zone in male, while the female has in addition three posterior groups of spines. A group of two or three spines present on either side of genital opening in the dorso-posterior protuberance. Variations in the number of spines on the posterior extremity are in some measure due to losses by mutilation.

Proboscis elongate, clavate, larger in female than in male, 1·06–2·97 mm. in length; anteriorly 0·178–0·341 mm., posteriorly 0·142–0·244 mm. in diameter. Proboscis hooks usually in fourteen longitudinal rows (range twelve to fifteen) with observed range of twenty-six to thirty-three hooks in each longitudinal row. Hooks on basal region of proboscis conspicuously modified and progressively more crowded proximally. On anterior region of proboscis hooks are widely spaced with distances of 70–82 μ between anterior margins of adjacent hooks, while near the base of the proboscis this space may be reduced to 12 or 18 μ. Limits of basal region marked by location of a pair of lateral papillae (Pl. XII, fig. 2). Basal proboscis hooks of three distinct types: those on lateral and ventral surfaces small, simple, thornlike, rarely exceeding 50 μ in length; six to eight ventral hooks of proximal circle greatly enlarged, 70–86 μ in length; four median-dorsal basal rows conspicuously differentiated as strongly recurved hooks, much heavier than those in adjacent rows but becoming gradually less specialized toward the base of the proboscis. In males the modified dorsal hooks in the basal region are 20–31 μ in length, while the ventral hooks of corresponding level are 30–46 μ long. In females the modified dorsal basals are 26–36 μ long, with corresponding ventral hooks 30–56 μ. Hooks on distal region of proboscis, anterior to the lateral papillae, show some dorso-ventral differentiation in form and size. Near tip of proboscis hooks on females average slightly larger (51–89 μ) than on males (51–77 μ) and show slight dorso-ventral difference in size. Near middle of proboscis ventral hooks

somewhat more recurved than dorsals, therefore appearing shorter (ventrals of males 36–66 μ, females 46–77 μ; dorsals of males 40–71 μ, females 36–86 μ).

Proboscis receptacle somewhat longer than the proboscis. Brain (Pl. XII, fig. 2) located within proboscis, anterior to the receptacle at the level of the basal hooks on the proboscis. Retinacula pass through the walls of the receptacle distinctly posterior to the location of the brain, nearly midway of the length of the receptacle. This location of the retinacula is unique, so far as the writers have been able to determine, for usually these organs pass directly through the wall of the receptacle in the immediate region of the brain. The condition in *Illiosentis furcatus* is apparently associated with the unusual location of the brain far anterior to its customary position.

A papilla on each lateral surface of the proboscis is located at about the level of the eleventh hook from the proximal region of the proboscis. These papillae seem to be homologous with the "Halspapille" described and figured by Meyer (1932–3, pp. 199 *et seq.*) for various genera of Archiacanthocephala. Though similar papillae have not been previously mentioned for any of the Palaeacanthocephala, the senior author of this paper has unpublished records of their occurrence in several undescribed species of Rhadinorhynchidae. The position in *Illiosentis* is distinctly in the proboscis and not in the neck as specified by Meyer in his descriptions of various Oligacanthorhynchidae, Moniliformidae and Pachysentidae. As in the case of the retinacula this unusual location seems to be directly associated with the anomalous location of the brain in *Illiosentis*.

Lemnisci long, cylindrical, about 1·5 times the length of the proboscis receptacle, and in males commonly to or near the anterior testis.

Male genitalia confined to posterior half of body. Testes broadly contiguous, followed by a series of eight elongate, pyriform to clavate cement glands.

Embryos within gravid females 67–74 μ long by 8–10 μ in maximum diameter.

Holotype male 3043·11 and allotype female 3346·5 in collection of H. J. Van Cleave. Paratypes in the collections of both authors and deposited in U.S. National Museum (Cat. No. 9270).

Host. Menticirrhus americanus (Linn.), in intestine.

Locality. Grand Isle, Louisiana, June and July 1936, and July 1938.

There are two references in the literature to the occurrence of "*Rhadinorhynchus pristis*" in *Menticirrhus americanus*. Meyer (1932–3, p. 347) cites a questioned determination of this species without comment as to source of the record. Linton (1905, p. 398) lists "*Echinorhynchus pristis*" as a parasite of *Menticirrhus americanus* in the vicinity of Beaufort, North Carolina, but he gives neither description nor drawings which would establish the identity of the form encountered. It is at least possible that both of these references are to materials belonging to the genus *Illiosentis*.

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EXPLANATION OF PLATE XII

Illiosentis furcatus n.g., n.sp.

All figures drawn with a camera lucida. The scale in Fig. 1 is 1 mm. long; in Figs. 2 and 3, 0·5 mm.; in Fig. 4, 0·1 mm.

Fig. 1. Holotype male, showing arrangement of organs.

Fig. 2. Proboscis of a paratype female showing details of hook arrangement, the location of the brain adjacent to the enlarged ventral hooks at the base of the proboscis, and the two lateral papillae (one of which belongs on the opposite lateral surface but is here shown as it appears when focusing through the proboscis).

Fig. 3. Posterior extremity of a paratype male showing particularly the number and arrangement of the cement glands and extruded bursa.

Fig. 4. Posterior extremity of allotype female, showing the two characteristic protuberances separated by a cleft, the wall of which contains a conspicuous fan of muscle.

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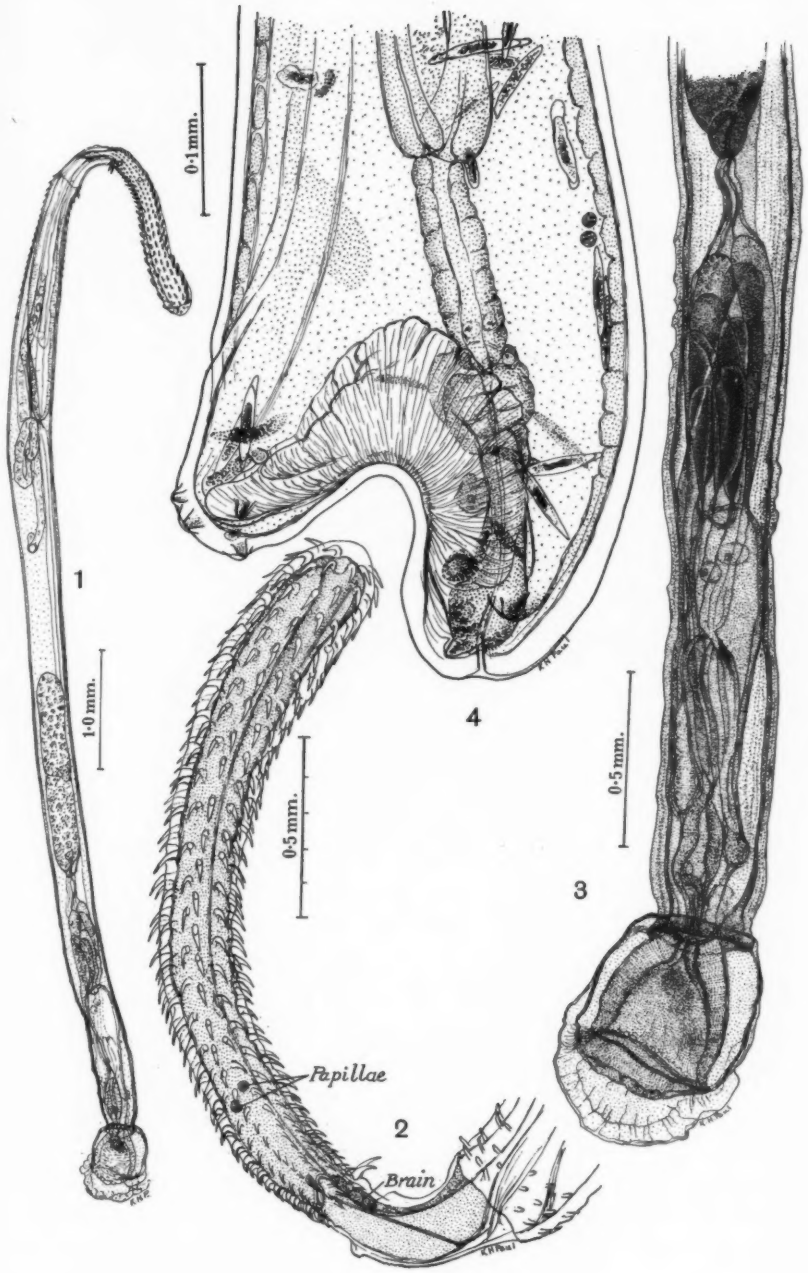

UNIV. OF MICH.

STUDIES ON THE GERM CELL CYCLE OF THE DIGENETIC TREMATODE *PARORCHIS ACANTHUS* NICOLL

PART I. ANATOMY OF THE GENITALIA AND GAMETOGENESIS IN THE ADULT

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(With 69 Figures in the Text)

Introduction

The unique life history of the digenetic trematodes has from time to time given rise to much controversy, various theories having been advanced to explain the origin and subsequent development of the germ cells contained in the various larval stages. These theories have been grouped by Brooks (1930) under the five headings metagenesis, heterogeny, paedogenesis, extended metamorphosis, and germinal lineage. The modern tendency is to accept the last named of these theories, but a considerable amount of further work is necessary, involving a large number of species before this interpretation of the life history can be applied to the whole group.

Very little is known of the chromosomes in the Trematoda. They have been mentioned in some early investigations of maturation phenomena by Halkin (1902), Kathariner (1904), Schubmann (1905), Goldschmidt (1905 and 1908), Dingler (1910), Schellenberg (1911), von Kemnitz (1913), Gille (1914), and Pennypacker (1936). Early workers recorded the chromosomes in the adult stage only, Cary (1909) being the first to report them from the larval stages. More recent studies are those of Cable (1931, 1934) on the germ cycle in *Cryptocotyle lingua*, and of Pin-Dji Chen (1937) on the germ cell cycle of *Paragonimus kellicotti*. Both these writers found maturation to occur only in the adult stage, while in the larval stage they found simply a multiplication of germ cells by ordinary mitotic division of the diploid chromosomes.

A detailed account of the literature on the subject is given by Brooks (1930) and Cable (1931, 1934), and need not be repeated here. But there is a considerable field for study in the chromosomes of digenetic trematodes, and it was thought that an investigation into the germ cells of a single species would be a contribution to the subject. *Parorchis acanthus* forms excellent material for such a study, as the eggs undergo maturation, fertilization, and cleavage, in the foremost part of the uterus, and develop so rapidly that by the time they reach the middle of the uterus each egg contains a fully formed miracidium.

Parorchis acanthus was first described by Nicoll as *Zeugorchis acanthus* in 1906. In 1907 he redescribed the species more fully and changed the generic name to *Parorchis, Zeugorchis* having been used by Stafford for a digenetic trematode in 1905. Nicoll's description is adequate in most respects, but as a preliminary to the study of gametogenesis it was felt that a detailed examination of the genital organs and the course of the genital ducts particularly of the female, was essential. The male and female genitalia, therefore, are described below, followed by an account of spermatogenesis and oogenesis in the adult. The development of the miracidium and of the succeeding larval stages is in process of investigation and will, it is hoped, appear at a later date.

Material and technique

Parorchis acanthus was obtained from the bursa Fabricii of the herring gull *Larus argentatus* Pont. The young stage of *Parorchis acanthus* is *Cercaria purpurae* Lebour, which occurs abundantly in *Nucella* (*Purpura*) *lapillus* on the shore at Aberystwyth providing a constant source of infection.

Specimens were fixed in Carnoy's or Gilson's fixative. Serial sections were cut ranging in thickness from 5 to 8 μ and stained with Heidenhain's haematoxylin and orange G, or with Ehrlich's haematoxylin and eosin, the former gave the better results for spermatogenesis and the latter for oogenesis.

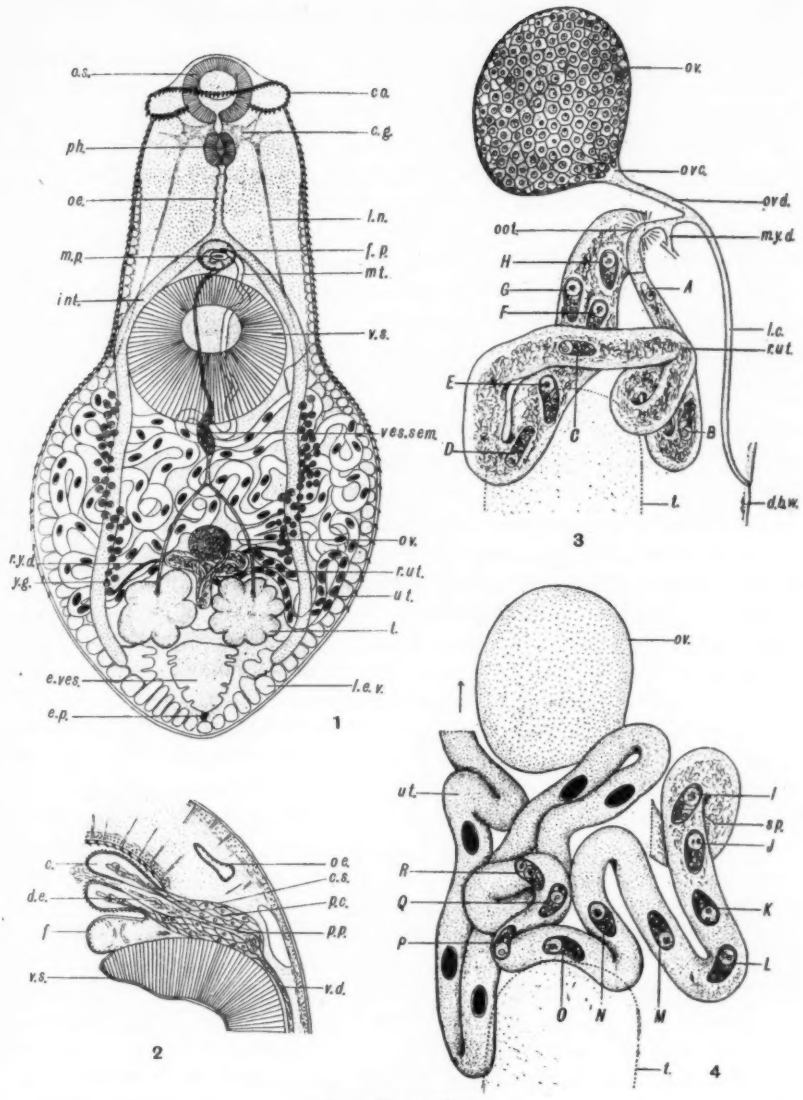
Observations were made with a $\frac{1}{12}$ in. oil immersion objective, and a $\times 20$ ocular, illumination was obtained from a 100 W. and where necessary a 500 W. lamp. All drawings have been made with a camera lucida.

Genital system of *Parorchis acanthus*

The male and female genital pores open into a shallow genital atrium immediately behind the bifurcation of the oesophagus and 0·14 mm. in front of the ventral sucker. The male aperture is to the right, and the female to the left and slightly in front of the male. The species is protandrous.

(1) *Male genital system*

There are two testes situated side by side near the posterior extremity of the body, immediately in front of the excretory vesicle (Fig. 1). They are dorso-ventrally flattened with a lobed margin, and measure 0·6–0·7 mm. in diameter. Both vasa deferentia arise antero-ventrally from near the centre of their respective testes. They run forwards towards the dorsal side, and a short distance behind the ventral sucker they unite to form an oval or spindle-shaped vesicula seminalis measuring 0·31 mm. in length and 0·1 mm. in breadth, which lies in the middle line and extends for a short distance forwards, dorsal to the posterior margin of the sucker. The median vas deferens then leaves the vesicula seminalis and continues forwards slightly to the right of the middle line to enter the cirrus sac at the anterior margin of the sucker (Fig. 2). The cirrus sac is not well defined, it is a thin walled cylindrical structure 0·09 mm. in diameter which runs obliquely antero-ventrally towards the genital atrium.



Parorchis acanthus

Fig. 1. General anatomy from ventral surface. Uterus simplified for clarity. × 15.

Fig. 2. Longitudinal section through evaginated cirrus. × 60.

Figs. 3, 4. Reconstruction of female genital ducts, from the left side. × 100.

Fig. 3. Origin of oviduct, Laurer's canal, yolk duct, ootype, and early part of receptaculum uterinum. × 100.

Fig. 4. Continuation of Fig. 3, showing the transition from receptaculum uterinum to uterus proper. × 100.

Fig. 4 should be superimposed on Fig. 3 as it occurs to the left in the entire animal, the dotted line indicates the point of junction. Eggs in stages of development are represented as they occur along the early part of the uterus, and are lettered *A*–*R*. These letters will be referred to again in the figures on oogenesis. For lettering see p. 432.

The median vas deferens enters the cirrus sac posteriorly and becomes continuous with the pars prostatica, a slightly wider tube 0·032 mm. in diameter, lined by a layer of well-defined cells. It takes a slightly sinuous course through the centre of the sac occupying about one third of its length. Into the pars prostatica open the unicellular prostatic glands. Distally the pars prostatica becomes continuous with the ductus ejaculatorius, a thin walled tube 0·045 mm. in diameter occupying the central region of the cirrus sac, and opening distally into the cirrus, a muscular evaginable organ 0·21 mm. in length and 0·15 mm. in breadth. It is covered by a cuticle armed with numerous delicate spines measuring up to 0·015 mm. in length. Spermatozoa are stored in the vesicula seminalis; they often fill up the median vas deferens and collect again in the ejaculatory duct which is slightly dilated for the purpose.

(2) *Female genital system*

The ovary is situated a short distance in front of the testes and more or less in the middle line (Fig. 1). It is transversely oval in outline and measures 0·29 × 0·33 mm. The oviduct arises from the postero-dorsal margin of the ovary, its initial portion forming a funnel-shaped ovicap. The oviduct measures 0·025 mm. in diameter, it passes almost directly dorsally and as it nears the dorsal body wall loops round to extend for a short distance ventrally and almost parallel to itself (Fig. 3). Just at the point where it bends there arises Laurer's canal, a narrow tube which runs posteriorly to open on the dorsal surface slightly to the right of the middle line 0·3 mm. behind the ovary. Just beyond the origin of Laurer's canal the median yolk duct enters the oviduct on its posterior border. The portion of the oviduct following this constitutes the ootype; it is not sharply demarcated but is surrounded by numerous unicellular pear-shaped shell glands which open into it. The shell glands together form a spherical mass 0·17 mm. in diameter which envelops the oviduct, median yolk duct and to a certain extent Laurer's canal at their points of junction. From the ootype the uterus turns posteriorly and pursues the course illustrated in Figs. 3 and 4. There is no receptaculum seminis, instead, the uterus fulfils the function of storing sperms along a considerable part of its length forming a so-called "receptaculum uterinum". The receptaculum uterinum begins immediately beyond the ootype; it is composed of the first few coils of the uterus and reaches a maximum diameter of 0·10 mm. before it becomes the uterus proper. It is filled with spermatozoa which have presumably entered through the female genital aperture and collected there before any ova were liberated from the ovary. In mature specimens ova in various stages of maturation are found amongst the spermatozoa in the receptaculum uterinum (Figs. 3, 4). The course taken by this early part of the uterus is not always absolutely constant; it is much less extensive in young individuals than in older ones where there are usually two descending loops, a dorsal and a ventral, between the anterior borders of the testes, and a loop on either side in front of each testis. The maximum diameter of the uterus proper is 0·073 mm.,

slightly less than that of the receptaculum uterinum at its widest part. It winds about in the post-acetabular region of the body, being confined to the area between the ventral sucker and the testes, and extends outwards beyond the level of the intestinal limbs to the lateral margins of the body, although here again its extent depends on age. In younger specimens it does not reach beyond the intestinal limbs even though it may contain fully developed eggs. At the posterior margin of the ventral sucker the uterus passes into the metraterm which runs forwards dorsally, and slightly to the left of the middle line to open by the genital aperture.

In the receptaculum uterinum and early part of the uterus the eggs are in process of maturation and segmentation. They stain deeply, and measure 0·08 × 0·044 mm. Development is very rapid and by the time the middle of the uterus is reached the eggs contain the fully formed miracidia. They have by this time increased in size to 0·10 × 0·06 mm. and are provided with a shell of a light yellow colour through which the miracidium with its X-shaped pigmented eye spot can easily be distinguished. The miracidia escape from the eggs by a transverse fissure at one end, either immediately before or just after they leave the parent worm.

The yolk glands are not very extensive. They consist of a row of follicles on each side of the body extending from the posterior margin of the ventral sucker to the level of the testes, not necessarily symmetrically on each side (Fig. 1). The transverse yolk ducts run obliquely towards the middle line curving dorsally to join together to form a short median yolk duct which opens into the posterior side of the oviduct. No conspicuous yolk reservoir has been observed. The yolk follicles are thin walled and each contain several yolk cells. These latter have well developed nuclei, yolk granules, and yellowish globules of shell-forming substance in their cytoplasm (Fig. 35).

GAMETOGENESIS IN *PARORCHIS ACANTHUS*

The diploid number of chromosomes in *Parorchis acanthus* is twenty-two, the same number as that recorded by Pennypacker (1936) for *Pneumonoeces medioplexus*, the largest number so far reported for a trematode. Goldschmidt (1908) and Dingler (1910) record twenty for *Dicrocoelium dendriticum*, von Kemnitz (1913) twenty for *Brachycoelium salamandrae*, Levy (1914) eighteen for *Distomum turgidum*, Pin-Dji Chen (1937) sixteen for *Paragonimus kellicotti*, and so on.

During gametogenesis the chromosomes do not appear in their typical shape, they are all more or less uniformly oval, they revert to normal appearance at fertilization.

(1) *Spermatogenesis*

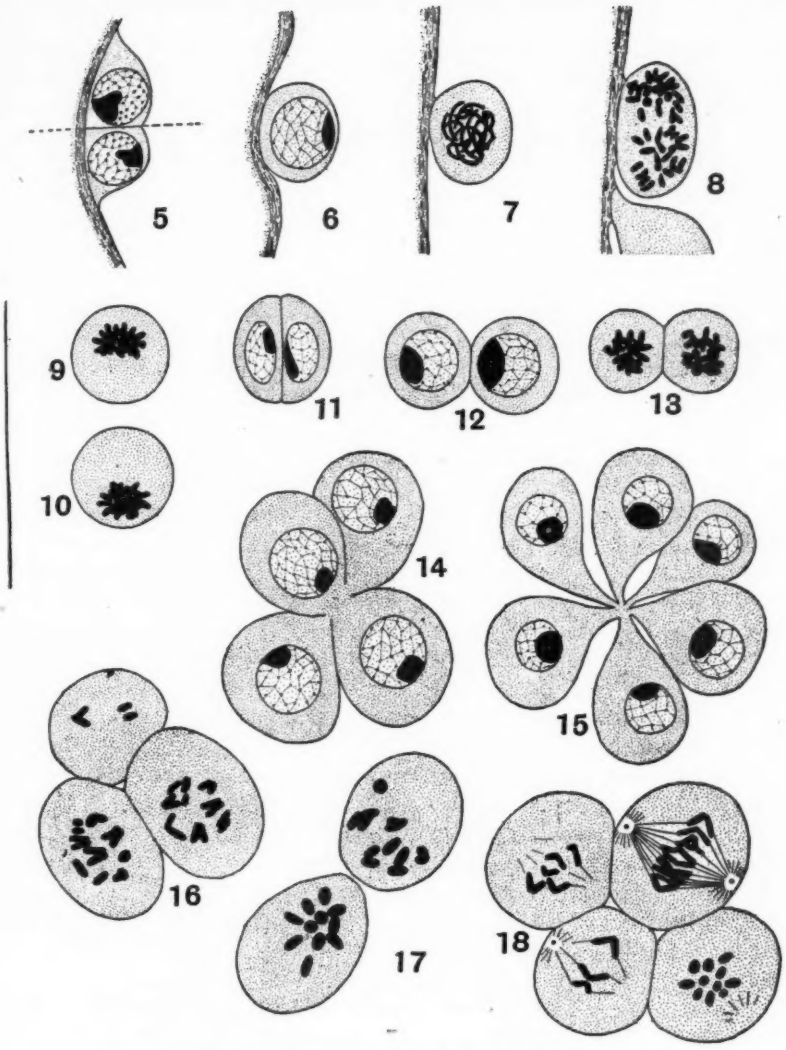
Primary spermatogonia. The primary spermatogonia (Fig. 5) form a layer of cells around the periphery of the testis attached to the testicular wall. They measure 0·005 mm. in diameter and possess a relatively large spherical nucleus

and very little cytoplasm. The resting nucleus has the usual appearance and contains a single conspicuous nucleolus in its nuclear sap. The chromosomes are invisible during the resting stage, according to White (1937) they are so highly hydrated that their refractive index is practically the same as that of the nuclear sap. The primary spermatogonium grows in size and becomes rounded, so that its connexion with the wall of the testis is restricted and it protrudes into the cavity, the nucleus, too, increases in size (Fig. 6). As division approaches, the nuclear membrane and nucleolus disappear, and the beginning of prophase is evidenced by the twenty-two chromosomes becoming visible as elongated curved threads (Fig. 7). Towards the end of prophase the chromosomes become very much shorter and thicker and appear as oval bodies of more or less uniform size. The metaphase, or formation of the spindle could not be seen during the division of the primary spermatogonia, the chromosomes are so numerous that they almost fill up the cell completely. During anaphase the chromosomes separate into two groups each of twenty-two which move to opposite ends of the cell (Figs. 8–10). These two telophase groups then become surrounded by a nuclear membrane, and assume the appearance of a resting nucleus. The cell divides into two secondary spermatogonia.

Secondary spermatogonia. The secondary spermatogonia are at first hemispherical in shape, the two together forming a spherical mass, which separates from the wall of the testis and passes into its cavity. The secondary spermatogonia grow in size and become rounded, so that the connexion between them becomes narrower, the nuclei too enlarge and become spherical (Fig. 12). Both secondary spermatogonia then divide into two in the same way as the primary to give rise to a group of four tertiary spermatogonia which remain connected together centrally (Fig. 14).

Tertiary spermatogonia. The groups of tertiary spermatogonia grow in size and move towards the centre of the testis. They divide by ordinary mitotic division to give rise to a group of eight cells which are the primary spermatocytes. These are still connected together centrally, but with the increase in number the central connexions become finer and the cells pear-shaped with their spherical nuclei in their outer rounded portions (Fig. 15).

Primary spermatocytes. The primary spermatocytes undergo meiosis or reduction division. The first meiotic division has an elongated prophase in which the individual stages can be recognized. In the leptotene stage the twenty-two chromosomes appear arranged at random in the cytoplasm of the cell. They are short oval bodies which during zygotene come together in pairs (Fig. 16). The pairing or synapsis begins at one extremity, spreads throughout the length of the chromosomes until the separate elements are no longer visible, and results in the pachytene stage where there are eleven bivalent chromosomes which are twice as thick and slightly shorter than the single leptotenes (Fig. 17). At metaphase the bipolar spindle makes its appearance in the cell. This is the only stage during spermatogenesis where the spindle is clearly visible; it may be because the primary spermatocytes are the largest cells, and the



Parorchis acanthus (spermatogenesis). ×2000.

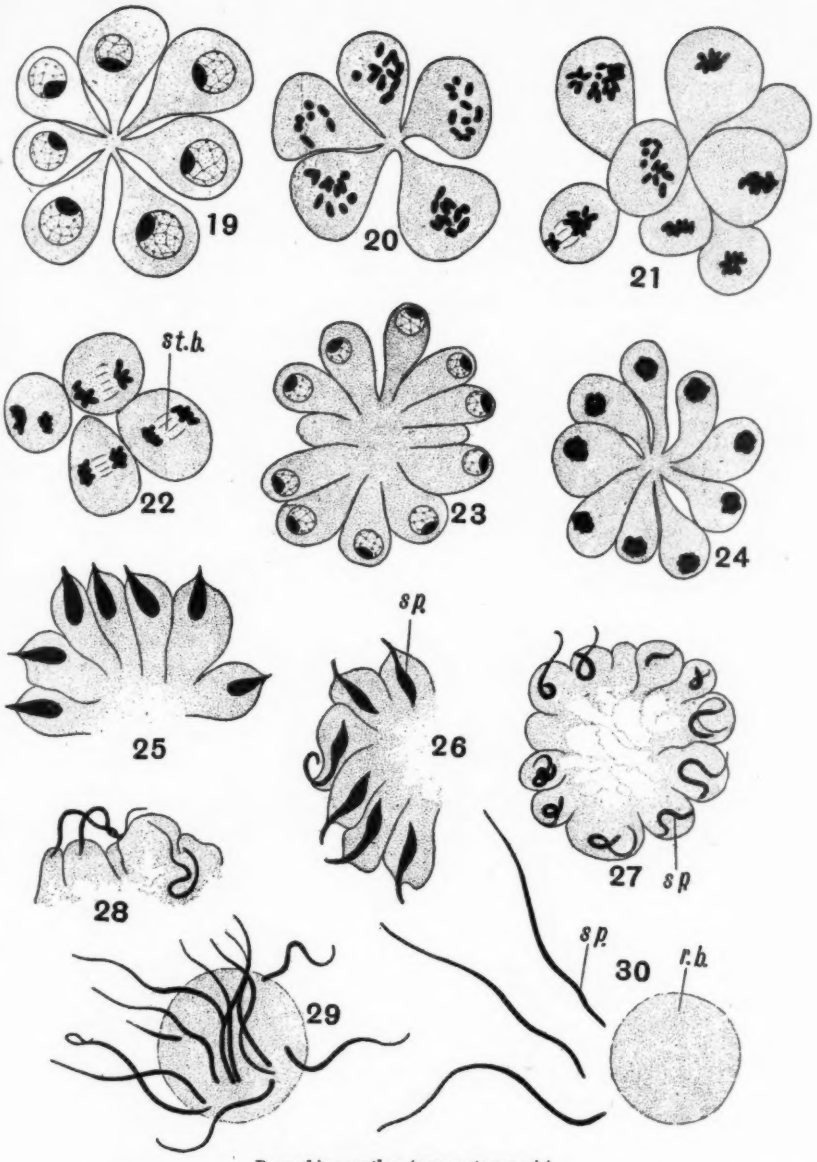
Fig. 5. Primary spermatogonia attached to wall of testis.
Fig. 6. Primary spermatogonium prior to division.
Fig. 7. Prophase of first mitotic division of primary spermatogonium.
Fig. 8. Anaphase of first meiotic division of primary spermatogonium.
Figs. 9, 10. Two sections of the same cell showing telophase of first meiotic division of primary spermatogonium.
Fig. 11. Two secondary spermatogonia.
Fig. 12. Two secondary spermatogonia prior to division.
Fig. 13. Late prophase in division of secondary spermatogonia.
Fig. 14. Four tertiary spermatogonia in resting stage.
Fig. 15. Eight primary spermatocytes in resting stage. (All eight not visible in the one section.)
Fig. 16. Zygotene of first meiotic division of primary spermatocyte.
Fig. 17. Pachytene of first meiotic division of primary spermatocyte.
Fig. 18. Anaphase of first meiotic division of primary spermatocyte.

chromosome number is less than in previous divisions. During anaphase the chromosomes separate into two groups which move towards the poles of the spindle. The spindle attachments are apparently terminal so that the distal ends of the chromosomes remain in contact for a time (Fig. 18). The eleven chromosomes arrived at the poles form, during telophase, two daughter nuclei which pass into the complete resting stage during interkinesis, and the cell divides into two secondary spermatocytes. All eight primary spermatocytes divide more or less simultaneously, and the result is a group of sixteen secondary spermatocytes all in the resting stage (Fig. 19). The individual cells are smaller than the primary spermatocytes as growth from now on does not keep pace with nuclear division.

Secondary spermatocytes. The prophase of the second meiotic division is very short, and differs from the ordinary mitotic prophase in that only eleven chromosomes appear in the cytoplasm (Fig. 20). After the formation of the spindle the chromosomes, which have previously split longitudinally, separate, eleven going to each pole (Figs. 21, 22), where they give rise each to a telophase nucleus, and the cell divides into two. The thirty-two spermatids thus formed still remain connected together centrally (Fig. 23).

Spermatids. The spermatids without further division give rise to the spermatozoa. In each case the nuclear membrane disappears and the chromatin forms an irregular mass, in which the individual chromosomes cannot be distinguished (Fig. 24). At the rounded end of each cell a projection is formed. The chromatin mass becomes elongated and pear-shaped, the narrow end protruding through the projection from the cell (Fig. 25). It is doubtful if the cytoplasm takes any part in the formation of the tail of the spermatozoon. The developing sperm elongates slowly, becoming proportionately narrower, and protrudes further from the cell, the part remaining inside being coiled (Figs. 26, 27). This gradually uncoils, pushing the sperm further out until finally it leaves the cytoplasm altogether and becomes free in the cavity of the testis (Figs. 28–30). The cytoplasmic mass having shed its thirty-two spermatozoa, shrinks and loses its original lobed appearance, the boundaries between the cells disappear and it forms a spherical body. These residual cytoplasmic bodies are scattered about in older testes.

The fully formed spermatozoa are slender deeply staining bodies with a head end tapering gradually to a long slender tail. They swim about in the spermatic fluid for a time, pass along the vas deferens and collect in the vesicula seminalis, median vas deferens and pars prostatica. They are transferred by the cirrus into the metraterm of another worm, when they travel down the uterus to collect in its proximal part or receptaculum uterinum to await the arrival of the ova. No spermatozoa have been observed in the oviduct or Laurer's canal.



Parorchis acanthus (spermatogenesis)

Fig. 19. Sixteen secondary spermatocytes in resting stage. (All sixteen not visible in the one section.)
Fig. 20. Prophase of second meiotic division of secondary spermatocyte.
Fig. 21. Late anaphase of second meiotic division of secondary spermatocyte.
Fig. 22. Telophase of second meiotic division of secondary spermatocyte.
Fig. 23. Thirty-two spermatids. (All thirty-two not visible in the one section.)
Fig. 24. First stage in formation of spermatozoa.
Figs. 25–29. Stages in elongation of spermatozoa.
Fig. 30. Fully formed spermatozoa and residual body.

(2) *Oogenesis*

Oogonia. The resting oogonia form a layer of small cells 0·0045 mm. in diameter lining the wall of the ovary over the whole of its internal surface. Each has a spherical nucleus with a well developed nucleolus and a little cytoplasm (Fig. 31). The oogonia divide by ordinary mitotic division to give rise to the oocytes.

Oocyte. The oocytes separate from the wall of the ovary, and grow rapidly in size as they pass towards the centre. In the centre and near the point of origin of the oviduct they are fully grown. Throughout the greater part of the ovary the oocytes are so closely packed together that they assume a polygonal shape (Fig. 32), but near the ovicap they are more loosely arranged and take on an oval outline (Fig. 33). A fully grown resting oocyte in the centre of the ovary has a diameter of 0·028 mm. several times that of the oogonia, with a well developed nucleus 0·018 mm. in diameter.

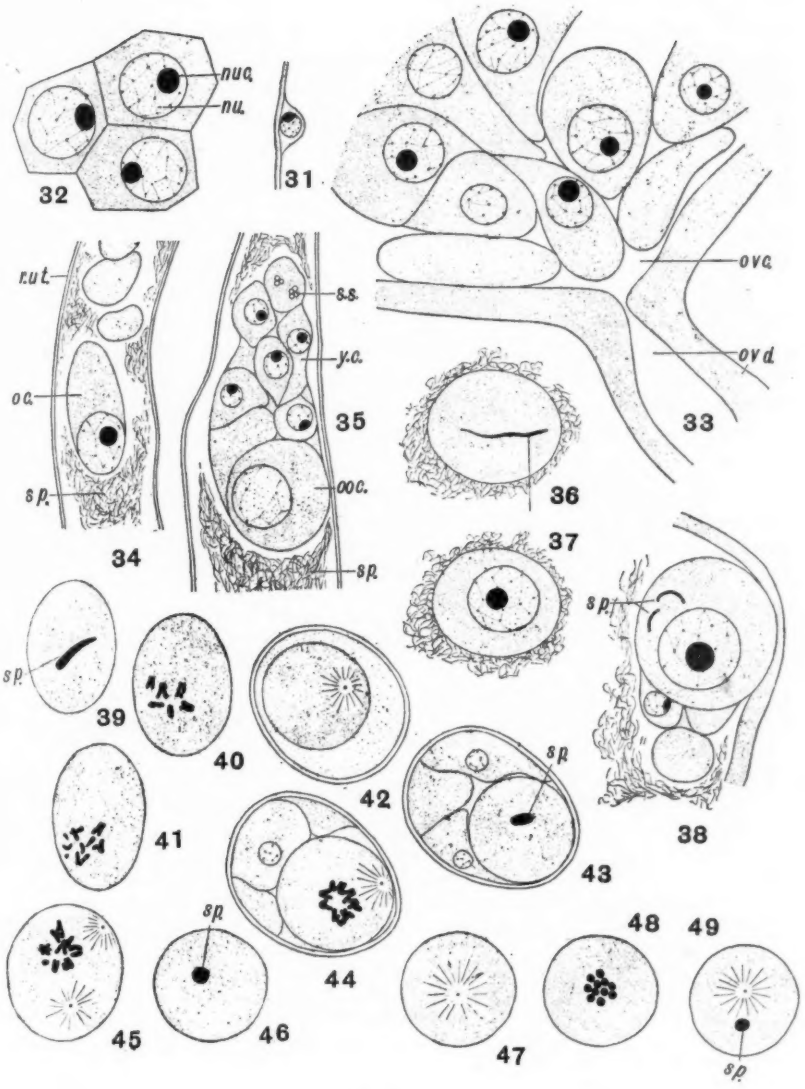
The oocytes are liberated singly through the ovicap into the oviduct. They travel along the oviduct, round the bend past Laurer's canal and the yolk duct into the ootype, and from there into the receptaculum uterinum where they meet the spermatozoa (Figs. 33, 34). Yolk cells which have entered the oviduct through the median yolk duct follow the oocytes closely, but do not become applied to them immediately. The application of yolk cells takes place at the first loop of the uterus, and in all cases observed, before the entry of the spermatozoon. The yolk cells collect on the posterior side of the oocyte and arrange themselves in the oval shape of the future egg, but the shell is not yet formed (Fig. 35). They are large cells with well developed nuclei each with a conspicuous nucleolus. Globules of shell-forming substance occur in the cytoplasm.

Legends to Figs. 31–49

Parorchis acanthus (oogenesis) ×750

(Yolk cells and shell not represented in Figs. 39–41, and 45–9)

Fig. 31. Oogonium attached to wall of ovary.
Fig. 32. Fully grown oocytes from centre of ovary.
Fig. 33. Oocytes near ovicap and origin of oviduct.
Fig. 34. Oocyte travelling down receptaculum uterinum and meeting spermatozoa. (*A* in Fig. 3.)
Fig. 35. Oocyte with yolk cells. (*B* in Fig. 3.)
Figs. 36, 37. Two sections of same cell showing spermatozoon, and oocyte nucleus. (*C* in Fig. 3.)
Fig. 38. Spermatozoon in cytoplasm of oocyte.
Figs. 39–41. Three sections of same cell showing zygotene of first meiotic division, and spermatozoon undergoing concentration. (*D* in Fig. 3.)
Figs. 42–44. Three sections of same egg showing zygotene of first meiotic division, appearance of centrosome, and further concentration of spermatozoon. (*E* in Fig. 3.)
Figs. 45, 46. Two sections of same cell showing zygotene, and spermatozoon now spherical. (*F* in Fig. 3.)
Figs. 47–49. Three sections of same cell showing the eleven bivalent chromosomes at metaphase, the two poles of the spindle, and the spermatozoon. (*G* in Fig. 3.)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sp.

Figs. 31–49

As soon as the oocyte has collected its yolk cells, a spermatozoon penetrates the cytoplasm, decreases slightly in length, and lies beside the oocyte nucleus which is as yet unchanged (Figs. 36, 38). Even though the whole egg is surrounded by a mass of sperms during its passage through the receptaculum uterinum, no case of polyspermy has been observed. Several sperms try to enter the egg, but never more than one has been observed in the cytoplasm. In Fig. 38 it is two portions of the same spermatozoon which appear in the section. Wassermann (1913) reports polyspermy in the eggs of *Zoogonus mirus*. The passage of the egg along the proximal part of the receptaculum uterinum is fairly rapid so that sperm penetration appears to occupy a greater proportion of its length than any other stage (Fig. 3—the length of the uterus between *B* and *D*).

Meiosis or maturation division. Just before maturation division takes place the shell appears as a thin layer surrounding the oocyte and yolk cells, and gradually thickening to its maximum as development proceeds. The passage of the eggs is now not so rapid as before, they tend to collect side by side in the widest part of the receptaculum uterinum, the ascending ventral loop.

The prophase of the first meiotic division is, as in the male, prolonged. At the beginning of the ascending loop of the receptaculum uterinum the nuclear membrane disappears from the egg nucleus, and at the leptotene stage the twenty-two short oval chromosomes appear in the cytoplasm. At zygotene these come together in pairs so that there are eleven stout bivalent chromosomes in the centre of the cell (Figs. 41, 44, 45 and 48). At metaphase the spindle makes its appearance and the eleven bivalents become attached to the equator of the spindle in which they are embedded, three or four occupying

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Legends to Figs. 50–69

Parorchis acanthus (oogenesis) × 750.

(Yolk cells and shell not represented in Figs. 50–56, and 60–63)

Figs. 50, 51. Two sections of same cell showing formation of first polar body, or late anaphase of first meiotic division. Spermatozoon enlarging. (*H* in Fig. 3.)

Figs. 52–54. Three sections of same egg showing early anaphase of second meiotic division, first polar body extruded, and spermatozoon resolved into chromosomes. (*I* in Fig. 4.)

Figs. 55, 56. Two sections of same egg showing telophase of second meiotic division second polar body, extruded first polar body, and spermatozoon. (*J* in Fig. 4.)

Fig. 57. Male and female pronuclei, and both polar bodies extruded. (*K* in Fig. 4.)

Fig. 58. Male and female pronuclei fully formed. (*L* in Fig. 4.)

Fig. 59. Nuclear membrane of pronuclei disappearing. (*M* in Fig. 4.)

Figs. 60, 61. Two sections of the same egg showing the eleven chromosomes appearing from each pronucleus. (*N* in Fig. 4.)

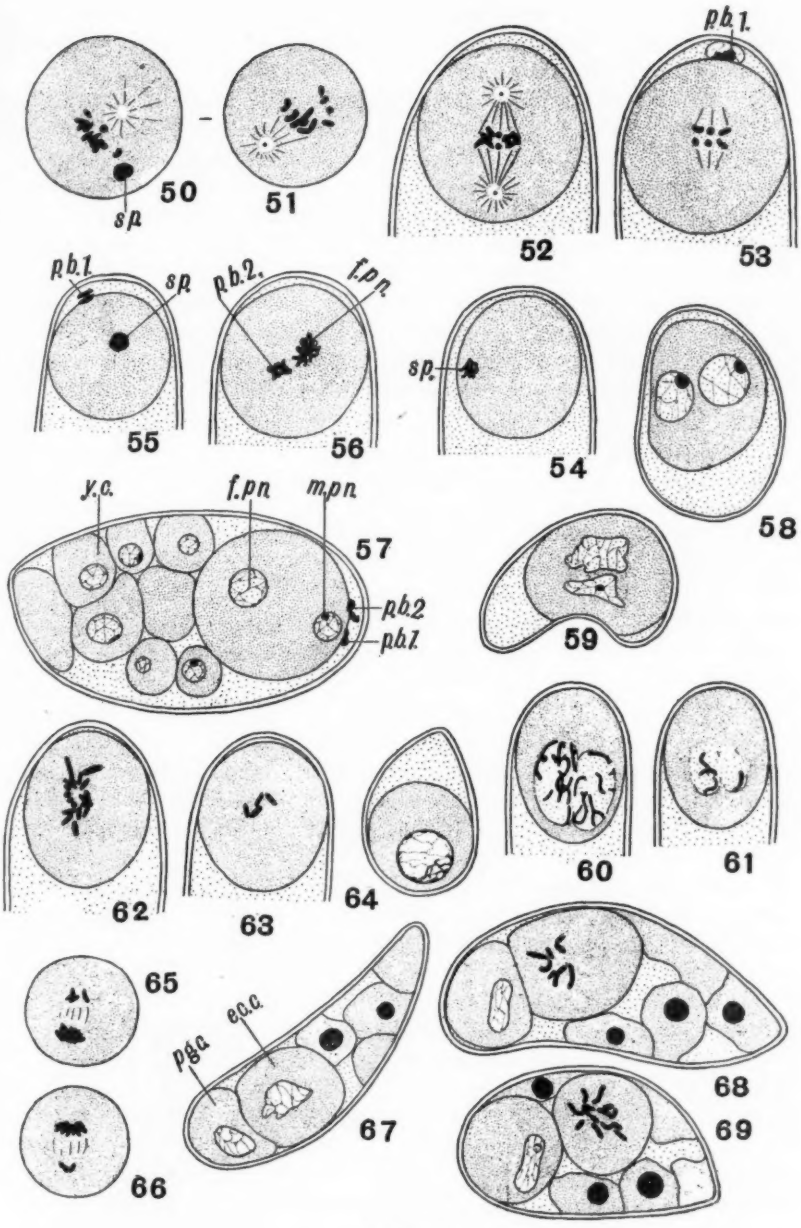
Figs. 62, 63. Fertilization. (*O* in Fig. 4.)

Fig. 64. Zygote nucleus in resting stage. (*P* in Fig. 4.)

Figs. 65, 66. Two sections of same cell showing telophase of first cleavage.

Fig. 67. Two cell stage. (*Q* in Fig. 4.)

Figs. 68, 69. Two sections of same egg showing prophase in division of "ectodermal cell", and "propagatory cell" undivided. (*R* in Fig. 4.)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50
51
pb.1.
52
53
pb.1
sp.
pb.2.
f.p.n.
55
56
sp.
54
58
y.c.
f.p.n.
m.p.n.
57
pb.2
pb.1
59
62
63
64
60
61
65
66
pga.
eo.c.
67
68
69

Figs. 50–69

the central region (Fig. 48). During the prophase and metaphase the spermatozoon, which on entry was thread-like, has contracted first into an oval and then into a spherical mass, and lies in the cytoplasm of the ovum outside the spindle (Figs. 39, 43, 46 and 49).

First polar body. At the anaphase of the first meiotic division the eleven bivalent chromosomes separate, eleven going to each pole of the spindle (Figs. 50, 51). One group persists and will give rise to the nucleus of the ovum, the other group forms the first polar body which moves to the surface of the ovum and is extruded from the cytoplasm. The stages of the first meiotic division occupy the ascending portion of the receptaculum uterinum (Fig. 3 *D–H*).

Second polar body. In the maturation of the female cell the chromosomes do not form a resting nucleus during interkinesis, but they remain condensed and undergo no change between the anaphase of the first division and the metaphase of the second. The prophase of the second meiotic division is therefore absent. The spindle of the second meiotic division appears immediately after the anaphase of the first, and the eleven chromosomes become attached to it at the equatorial plane. They have already split longitudinally at an earlier stage, and now separate, eleven going to each pole (Figs. 52, 53). One group moves towards the surface of the ovum and forms the second polar body which, like the first, is extruded from the cytoplasm. The other group forms the nucleus of the matured ovum, the female pronucleus (Figs. 55, 56). The telophase of the second meiotic division does not differ from that of ordinary mitosis, and the resting pronucleus is spherical with a well developed nucleolus. During maturation division the spermatozoon undergoes certain changes. With the formation of the first polar body it enlarges and the chromosomes begin to resolve themselves out, and are easily apparent as threads during the formation of the second polar body. The male pronucleus is formed simultaneously with the female pronucleus and is similar in structure. Both remain in the resting stage for a short time (Figs. 57, 58). The egg has now left the receptaculum uterinum and passed into the uterus proper (Fig. 4 *K*). Prior to fertilization, the nucleoli of both pronuclei gradually disappear, and the chromosomes finally become visible as two adjacent groups of eleven coiled threads (Figs. 60, 61). Fertilization takes place in an early loop of the uterus usually above the left testis (Figs. 4 *O*, 62, 63).

Cleavage begins almost immediately. The cell divides by ordinary mitotic division into two, one larger and one smaller cell (Figs. 65–67). According to Pin-Dji Chen (1937) Ishii found a corresponding condition in the first cleavage of the fertilized ovum of *Fasciolopsis buski*. He referred to the small cell as the "propagatory cell" and the large one as the "ectodermal cell". Pin-Dji Chen found the same thing to occur in the first cleavage of the egg of *Paragonimus kellicotti*.

The second cleavage concerns only the larger cell (Figs. 68, 69), and the result of the division is three cells, two "ectodermal" and one "propagatory".

Segmentation has not been followed beyond this stage as yet, but it is intended at a later date to trace the development of the miracidium and to investigate the germ cell cycle in the succeeding larval stages.

DISCUSSION

Gametogenesis in *Parorchis acanthus* resembles fairly closely that described by Pin-Dji Chen for *Paragonimus kellicotti*. In spermatogenesis and oogenesis of the adult, the first meiotic division is the reduction division. Pennypacker (1936) does not state exactly where reduction takes place in *Pneumonoeces medioplexus*, but as the primary spermatocytes and oocytes contain the haploid number, reduction must have taken place before these stages, that is, earlier than in *Parorchis acanthus*. The worm being hermaphrodite, the male and female cells have the same number of chromosomes. As observed by Linder (1914), a difference in number is apparent only in dioecious trematodes, e.g. *Schistosoma haematobium* Bilh.

Note on the synonymy of Parorchis acanthus *Nicoll, and* P. avitus *Linton*

Since Nicoll's original description a second species of the genus *Parorchis*, namely *P. avitus*, has been described by Linton (1914), from the cloaca of the same host *Larus argentatus* at Wood's Hole, Mass. There has been a certain amount of controversy as to whether this form is synonymous with *Parorchis acanthus* Nicoll. The two are strikingly similar in all details of their anatomy. The average measurements of four specimens differ slightly, those given by Linton for *P. avitus* being fairly consistently smaller than those of *P. acanthus*, but this seems to be due to a greater diversity of size between the individuals measured in the case of the former species. The proportions of the measured parts are the same.

Linton (1914) argues against the two being synonymous mainly on the extent of the uterus. He states that in *P. avitus* it is much more extensive than in *P. acanthus*, reaching to the margins of the body and for a short distance on each side of the ventral sucker and testes. However, in the present investigation, the uterus has been found to vary considerably in different specimens apparently with age, being much less extensive in younger forms. The uterus, therefore, is not a reliable feature to choose for specific differentiation.

Nicoll described the eggs of *P. acanthus* as opening by a longitudinal slit, while Linton finds a transverse slit in the eggs of *P. avitus*. In the present case the break seems to be transverse at one end of the egg as for *P. avitus*, but a few eggs do rupture longitudinally with pressure, which may have happened in the case of Nicoll's specimens.

The young stages of both, too, seem to be synonymous. *P. acanthus* has as its larval stage *Cercaria purpurae* from *Nucella lapillus*. In 1931 Stunkard and Shaw found a very similar cercaria, *Cercaria sensifera*, in *Urosalpinx cinereus*

also at Wood's Hole, Mass., and suggested that it might be identical with *Cercaria purpurae*, and also that it might be the larval stage of *Parorchis avitus*. A further examination of *Cercaria purpurae* (Rees, 1937) showed that the two are apparently identical, so that *C. sensifera* becomes a synonym of *C. purpurae*. A large number of *Urosalpinx cinereus* was very kindly sent from Liverpool by Prof. Orton, and of six hundred examined only one was found to be infected with *Cercaria purpurae*. In this country the favourite host seems to be *Nucella lapillus*.

It seems very likely, therefore, that the two species are identical and that *Parorchis avitus* is synonymous with *P. acanthus*.

Summary

1. The anatomy of the male and female genitalia of *Parorchis acanthus* is described in detail. An extensive receptaculum uterinum occurs in the female system.

2. The chromosome number in *P. acanthus* is twenty-two.

3. Spermatogenesis, oogenesis, and fertilization, are described in the adult worm. The chromosome number in both male and female cells is reduced to eleven at the first meiotic division.

4. Maturation in the female takes place in the "receptaculum uterinum".

5. Cleavage of the ovum to the three cell stage has been followed.

6. The probable synonymy of *P. acanthus* and *P. avitus* is discussed.

Key to Lettering of Figures

c.	Cirrus.	*ooc.*	Oocyte.
c.s.	Cirrus sac.	*oot.*	Ootype.
cg.	Cerebral ganglion.	*ov.*	Ovary.
co.	Collar.	*ovc.*	Ovicap.
d.b.w.	Dorsal body wall.	*ovd.*	Oviduct.
d.e.	Ductus ejaculatorius.	*p.b.* 1	First polar body.
e.p.	Excretory pore.	*p.b.* 2	Second polar body.
e. ves.	Excretory vesicle.	*p.c.*	Prostate gland cells.
ec. c.	"Ectodermal cell".	*p.p.*	Pars prostatica.
f.	Fold in front of ventral sucker.	*pg. c.*	"Propagatory cell".
f.p.	Female genital pore.	*ph.*	Pharynx.
f. pn.	Female pronucleus.	*r.b.*	Residual cytoplasmic body.
int.	Intestine.	*r. ut.*	Receptaculum uterinum.
l.c.	Laurer's canal.	*r.y.d.*	Right yolk duct.
l.e.v.	Lateral excretory vessel.	*s.s.*	Shell forming substance.
l.n.	Lateral nerve.	*sp.*	Spermatozoon.
m.p.	Male genital pore.	*st. b.*	"Stem body" of spindle.
m. pn.	Male pronucleus.	*t.*	Testis.
mt.	Metraterm.	*ut.*	Uterus.
m.y.d.	Median yolk duct.	*v.d.*	Vas deferens.
nu.	Nucleus.	*v.s.*	Ventral sucker.
nuc.	Nucleolus.	*ves. sem.*	Vesicula seminalis.
o.s.	Oral sucker.	*y.c.*	Yolk cell.
oc.	Oocyte.	*y.g.*	Yolk glands.
oe.	Oesophagus.		

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ON SOME TICKS BELONGING TO THE GENERA *APONOMMA* AND *AMBLYOMMA*

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(With 9 Figures in the Text)

A recent accession to the collection of the British Museum (Natural History) contains a number of ticks taken in 1927 from a captive Komodo dragon (*Varanus komodoensis*) in the Zoological Gardens, London. Figures of the two species of ticks concerned were prepared by Mr A. J. E. Terzi for the late Dr W. L. Sambon who intended to describe them as new but died before he had done so. The two species have since been described by other authors, but Mr Terzi's excellent figures are reproduced here (Figs. 1–4), together with a note on the synonymy of one of the species.

Besides these, some ticks were collected from a specimen of *Cyclura macleayi caymanensis* by Mr C. B. Lewis on the Oxford University expedition to the Cayman Islands. They are described here and seem to belong to the species *Amblyomma torrei* Vigueras which is known (in the male only) from *Cyclura macleayi* in Cuba. I am grateful to Dr L. E. Robinson for examining the specimens and giving me the benefit of his opinion: he points out their resemblance to *Amblyomma scutatum* Neumann. I am also indebted, for the loan of type material, to Dr A. C. Oudemans, Dr L. F. de Beaufort, Director of the Zoologisch Museum, Amsterdam, Prof. Keilin and Dr Tate of the Molteno Institute, Cambridge.

Aponomma komodoense Oudemans (Figs. 1, 2)

A. komodoense Oudemans, 1928.
A. draconis Warburton, 1933.

Material. 23 males, 9 females, 2 nymphs collected in the Zoological Gardens, London, in May 1927 and in November 1927, from *Varanus komodoensis*. One of the males is malformed.

In addition to the above material I have been able to examine 8 male co-types of *Aponomma komodoense* and male and female co-types of *A. draconis*. A comparison of the male specimens leads me to conclude that *draconis* of Warburton is synonymous with *komodoense* of Oudemans. They agree in the absence of lateral grooves, in the shape of cervical grooves, spiracles and capitulum, in the hypostomal dentition and in the coxal armature. On the last of these points it should be mentioned that Dr Oudemans's figure of the coxae is inaccurate: there are two blunt spurs on coxa I. The male co-type

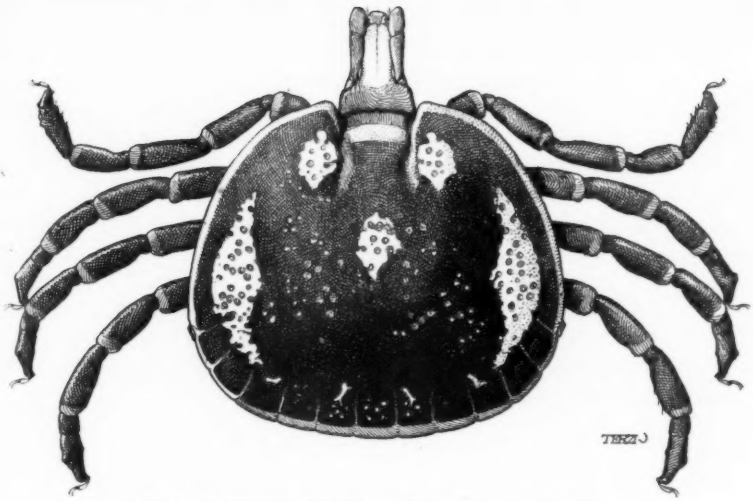

Fig. 1. *Aponomma komodoense* Oud., ♂, dorsal. ×*c.* 20.

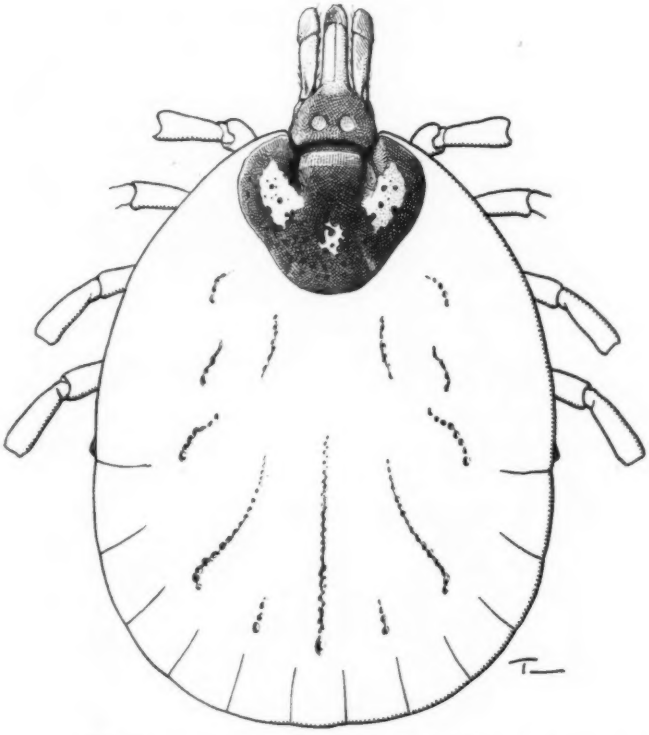

Fig. 2. *Aponomma komodoense* Oud., ♀, dorsal. ×*c.* 15.

of *draconis* differs from those of *komodoense* in having somewhat denser punctation and in not having the pale silvery spots beside the cervical grooves or the posterior row on the festoons. Both these characters, however, are found to be variable in the British Museum series; the ornamentation is especially so, and although the figured specimen has the cervical spots well developed, others have them reduced to a mere dot and in still others they are absent altogether. The distal end of the femora of all four legs in the male is tipped on the dorsal side with a silvery spot.

Amblyomma robinsoni Warburton, 1927 (Figs. 3, 4)

Material. 3 normal males; 1 dwarf male about half as large as the others, with deficient ornate pattern. Collected from *Varanus komodoensis* in the Zoological Gardens, London, May 1927.

Amblyomma torrei Vigueras, 1934 (Figs. 6–9)

Material. 3 males, 3 females, 10 nymphs found by Mr C. B. Lewis on *Cyclura macleayi caymanensis* Barbour & Noble, South Sound, Little Cayman, West Indies.

Male. Diagnosis. A small tick; scutum ornate with a pale brown, median longitudinal band between silvery lateral fields; marginal groove absent; eyes pale and flat; hypostome dentition 3/3; coxa I with two short spurs, coxae II to IV each with a short outer spur and a minute inner tubercle.

Description. Size: (1) Length 3·6 mm., width 3·3 mm.; (2) length 3·1 mm., width 2·6 mm.; (3) length 3·0 mm., width 2·9 mm. *Body:* contour oval, slightly broader posteriorly, the scapulae rather square. *Scutum:* convex; ornate, a median longitudinal band of pale brown with a silvery area on each side, the latter distinct from the scapulae to the level of the second festoon on each side, extending indistinctly round the posterior periphery with, in one specimen, a few irregular pale specks in the middle of the median brown zone; cervical grooves short, deep, kidney-shaped; lateral grooves absent; punctations numerous and of medium size in the peripheral zone, somewhat fewer and smaller in the median inornate field; eyes pale and flat. *Venter:* dull yellow in colour; genital aperture opposite the anterior margin of coxa II: spiracles (see Fig. 6A). *Capitulum:* Length 1·2 mm., basis rectangular, postero-lateral angles slightly salient, lateral margins convex; palpal article II twice as long as article III; hypostome dentition 3/3. *Legs:* coxa I with two short spurs, coxae II–IV each with a short external spur and a minute (hardly visible) inner tubercle.

Female. Diagnosis. A small tick; scutum somewhat cordiform but with square scapulae, broader than long; ornate with dark brown markings on a pale ground; punctations rather coarse, numerous, fairly regularly distributed; eyes pale and flat; porose areas small, oval, widely separated; hypostome dentition 3/3; coxa I with two short spurs, coxae II–IV each with a short outer spur and a very small, though distinct, inner spur.

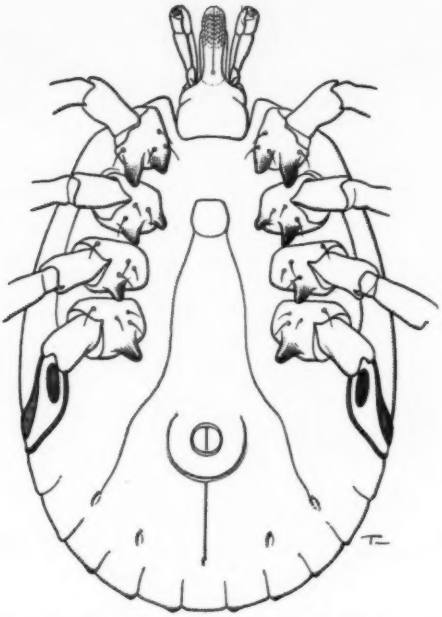

Fig. 3. *Amblyomma robinsoni* Warburton, ♂, ventral. ×*c.* 13.

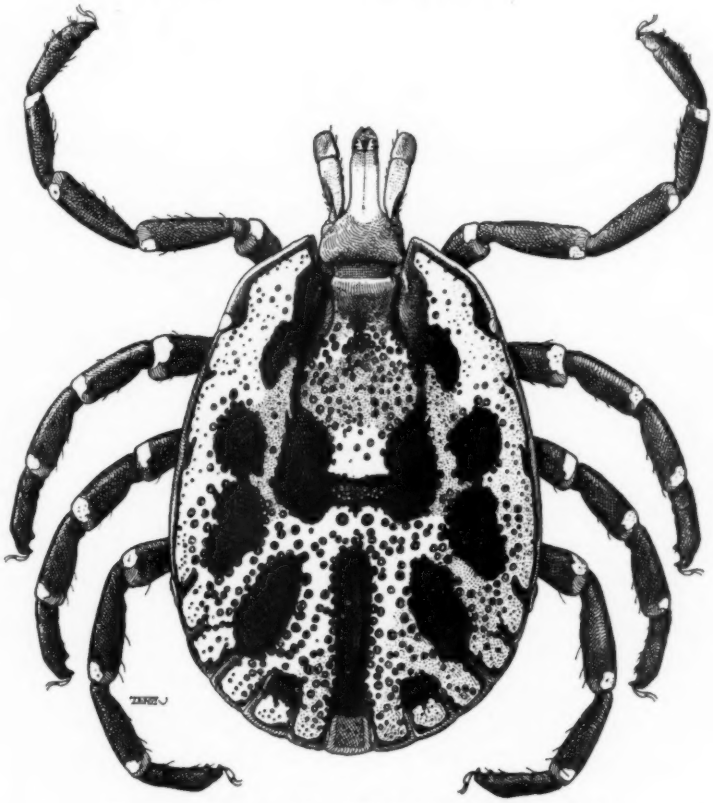

Fig. 4. *Amblyomma robinsoni* Warburton, ♂, dorsal. ×*c.* 12.

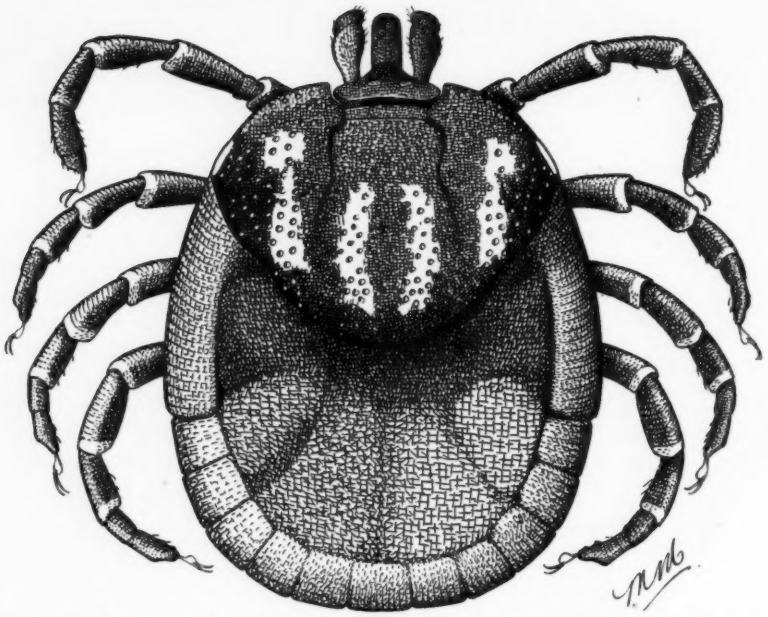

Fig. 5. *Amblyomma scutatum* Neumann, ♀ co-type, dorsal (Nuttall Collection No. 2876). ×22.

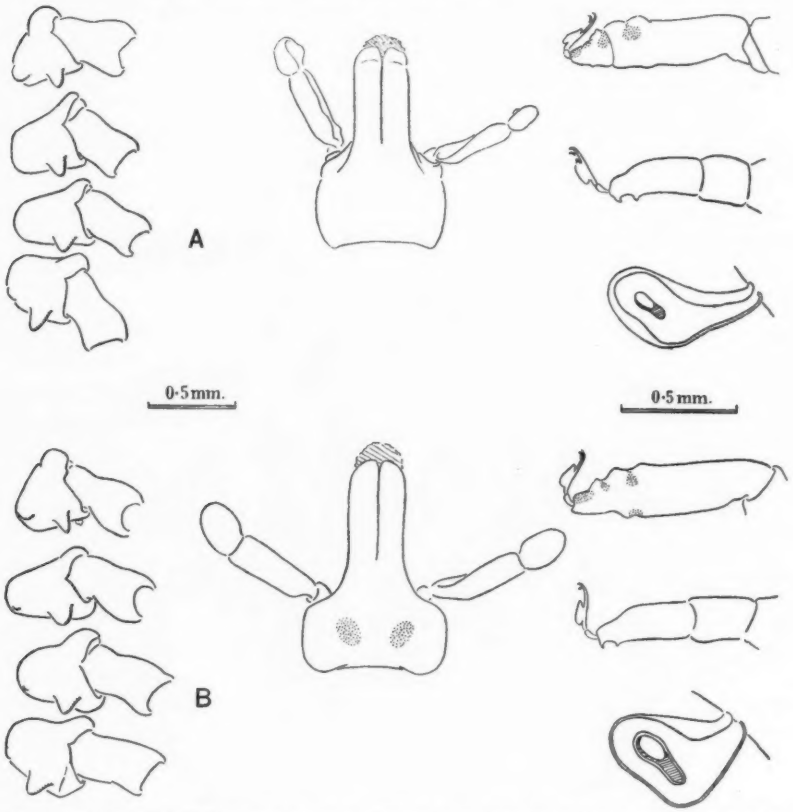

Fig. 6. *Amblyomma torrei* Vigueras, coxae, capitulum, tarsi I and IV, and spiracle; A of ♂, B of ♀.

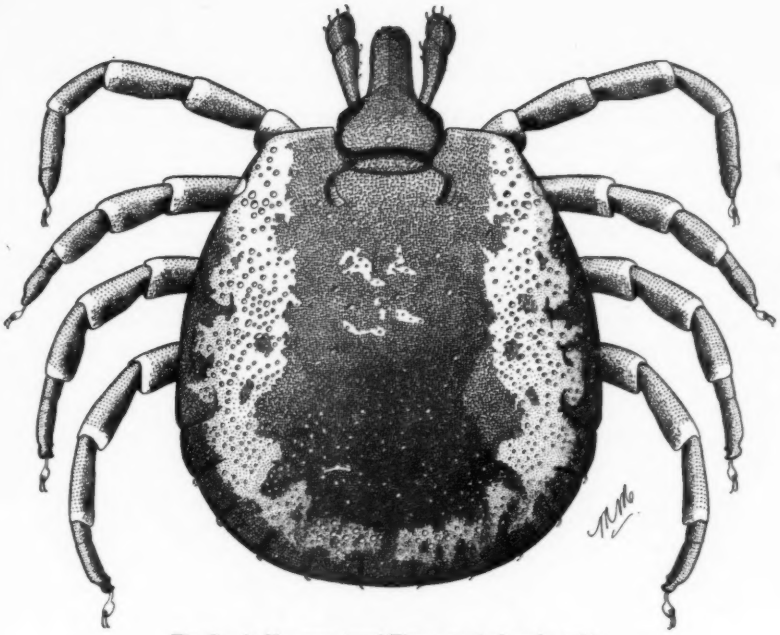

Fig. 7. *Amblyomma torrei* Vigueras, ♂, dorsal. ×20.

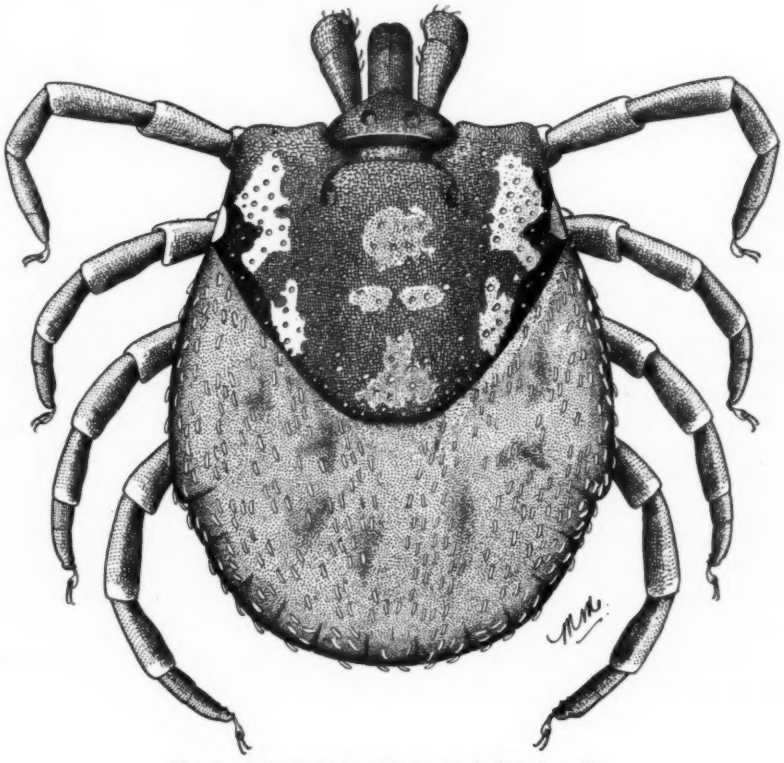

Fig. 8. *Amblyomma torrei* Vigueras, ♀, dorsal. ×22.

Description. Size: (1) Length 3·6 mm., width 2·9 mm.; (2) length 3·8 mm., width 3·3 mm.; (3) length 3·5 mm., width 2·9 mm. *Dorsum:* oval in contour, reddish brown in colour, beset with numerous short, blunt, whitish hairs in the region behind the scutum, more numerous than shown in Fig. 8; marginal groove absent; festoons well defined. *Scutum:* (1) Length 2·0 mm., width 2·4 mm.; (2) length 2·0 mm., width 2·6 mm.; (3) length 1·8 mm., width 2·3 mm.; somewhat cordiform in shape but with the anterior and antero-lateral edges almost straight and meeting at a slightly obtuse angle; ornate with dark brown markings on a pale ground (see Fig. 8); cervical grooves,

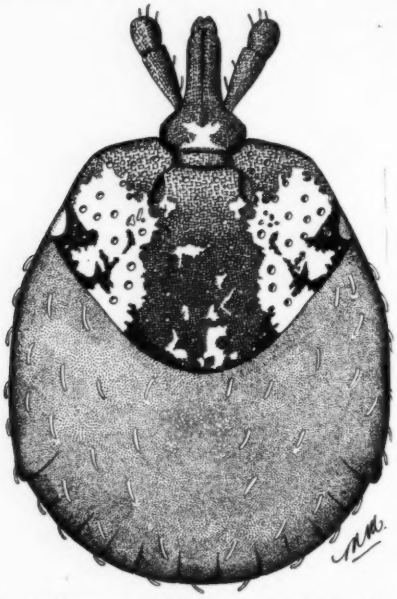

Fig. 9. *Amblyomma torrei* Vigueras, nymph, dorsal. ×38.

short, deep comma-shaped; punctations numerous, rather coarse, fairly regularly distributed; eyes pale and flat. *Venter:* paler in colour than the dorsum; genital aperture opposite the middle of coxa II; spiracles (see Fig. 6 B). *Capitulum:* length 1·2 mm., basis rectangular with convex lateral edges and slightly concave posterior edge; porose areas small, oval, widely separated; hypostome dentition 3/3. *Legs:* coxa I with two short spurs, coxae II–IV each with a short outer spur and a very small, though distinct, inner spur.

Nymph. Resembling the female in general; scutum with well-marked ornate pattern (see Fig. 9); scapulae less square than in the female, hairs on the dorsum more sparse. *Size:* length 1·4–2·2 mm., width 1·3–1·9 mm. *Scutum:* length 0·78–0·85 mm., width 0·93–1·2 mm.

The discovery of yet another species of *Amblyomma* with ornate nymphs is of interest (cf. Warburton, 1927; Bequaert, 1932).

The males agree fairly closely with the original description (which is, unfortunately, not illustrated) in size, ornate pattern, hypostomal dentition, coxal armature, and absence of lateral grooves but the five ventral plates are not observed in the British Museum material. The species is closely allied to *A. scutatum* Neumann (on lizards, Guatemala) of which I have been able to examine male and female co-types (Nuttall Collection, Molteno Institute, Cambridge) and four males (det. Neumann, 1905, British Museum (Natural History)). The males differ from those of *scutatum* in the rather square scapulae, in the deficient scutal ornamentation and in the presence of incipient internal spurs on coxae III and IV. The females are distinguished (cf. Figs. 5 and 8) by the square scapulae, the absence of marginal grooves, the short cervical grooves (which extend far back in *A. scutatum*), the presence of minute internal spurs on coxae II–IV and the presence of numerous hairs on the dorsum (*A. scutatum* being glabrous). In the incipient internal coxal spurs this species would seem to approach *A. cruciferum* Neumann (on *Cyclura stejnegeri*, Haiti: male, Robinson, 1926; female, Bequaert, 1932) which has two short spurs on coxae I–III: but the two species differ somewhat in the ornate pattern of both sexes and the females differ especially in the shape of the scutum and the form of the cervical grooves. It is noteworthy, however, that *A. cruciferum* is one of the species in which an ornate nymph is known and the female dorsum has "a few, irregularly scattered, short white hairs".

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ON THE LIFE HISTORY AND BIONOMICS OF *CHRYSOMYIA RUFIFACIES* MACQ. (ORDER DIPTERA, FAMILY CALLIPHORIDAE)

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During field collections of muscoid larvae in Calcutta, the "hairy maggots" of *Chrysomyia rufifacies*, which according to Froggat (quoted by Patton, 1922) has recently become a notorious pest of sheep in Australia, were encountered. The species is widely distributed in India and is mainly necrophagous in habits. Though the adult fly is not strictly speaking a house-frequenting insect, it is attracted by putrefying meat, and a few can often be captured in the house along with *Lucilia cuprina*, *Chrysomyia megacephala* and species of *Sarcophaga*. In the opinion of Patton (1922) its larvae prey on those of *Sarcophaga*, *Lucilia* and *Chrysomyia*, which also breed in decomposing animal remains.

While trying to breed out adults from larvae of all species of flies collected in nature, we were struck when we discovered that from three batches of larvae brought on different days and from different sources in November and December, adults of *Chrysomyia rufifacies* of one sex only were obtained; either they were all males or all females. This led us to investigate whether the absence of the other sex in a sample comprising a batch of larvae was due to the paucity in the number of specimens obtained in each collection or if it represented a phenomenon occurring in nature. We had not long to wait, as a gravid female was soon captured in the laboratory, being attracted by putrid meat. Meat was provided for oviposition. A number of larvae and pupae were killed and preserved and the remainder allowed to complete their development. Forty-five flies bred out, and as no apparent selection was exercised in the specimens that were killed, it was surprising to find that all were males. It was then decided to continue systematic observations on the subject.

Material and methods

In January seventeen males and three females were bred from larvae collected from a dead hawk. They were fed on meat juice, sugar and water, and the females were kept in separate cages for oviposition. Wild females caught at this time were also kept in separate cages.

Life history and bionomics

The observations recorded in this paper were made in Calcutta during winter and summer seasons, when the maximum temperature in the laboratory varied from 76 to 92° F.

A high-protein diet is usually necessary for the formation of eggs in flies. This has been demonstrated by a number of observers, e.g. by Roubaud (1922) in *Musca domestica*, by Cousin (1929) in *Lucilia sericata* and by Mackerras (1933) in *L. cuprina* and *L. sericata* and other blow-flies. The same fact holds good in *Chrysomyia rufifacies*, as when they are fed on sugar and water only the ovaries show a partial development, whereas the inclusion of meat juice in the diet will lead to complete development of eggs in about 5 days.

The development of the testes, on the other hand, is independent of diet, as spermatozoa can be detected in males immediately after their emergence.

Copulation takes place at rest and can even be performed in an ordinary test-tube. One male is capable of fertilizing at least five females. A single mating is sufficient for the deposition of at least three batches of eggs and perhaps more.

Ovulation can proceed independently of fertilization but oviposition cannot take place without fertilization, a fact which was also noted by Mackerras (1933). Eggs may be deposited in 24 hr. after mating, depending on the condition of the ovaries at the time of mating. In unmated females, when fed on meat juice, the abdomen after some time becomes distended with eggs, but they are never laid unless the female parent has had the chance to mate. After the death of the female, examination of the spermathecae showed the presence of sperms which proved that mating had taken place prior to deposition of eggs.

Eggs are usually laid after dusk and hatch during the night. In one particular instance a batch of eggs laid at 5 p.m. did not hatch before 1 a.m. next morning, when hourly examination ceased; at 5 a.m. larvae were found, the eggs having hatched between 8 and 12 hr. after they were laid.

As the contents of the ovaries are completely discharged at the time of oviposition, the number of eggs can be accurately determined from an examination of the ovaries of gravid females as was shown by one of us (Roy, 1938). In *C. rufifacies*, the average number deposited in the first batch by a laboratory-bred fly is about 210, 153 being the minimum and 386 the maximum.

The larval period lasts about 5 days; it takes another 4 days for the emergence of the adult. The period from egg to adult thus occupies about 9½ days. In Australia the life cycle occupies 15 days in summer (Mackerras, 1933).

Contrary to the descriptions of Patton (1922; Patton & Evans, 1929), the pharynx of the larva is provided with longitudinal ridges which are quite evident in a ventral view. According to Keilin (1912, 1915, 1917), the presence of well-marked ridges on the floor of the pharynx is indicative of a saprophagous habit,

while in carnivorous larvae these ridges are absent. Keilin (1912, 1917), Keilin & Tate (1930) and Muirhead Thomson (1937), have shown that in certain anthomyid larvae which are semi-carnivorous, the ventral surface of the basal piece bears distinct longitudinal ridges. Patton remarked that the larvae of *C. rufifacies* were voracious predators on other larvae, especially those of *Chrysomyia*, *Lucilia* and *Sarcophaga*. This possibly occurs when there is insufficient carrion. They will also turn to cannibalism when other food is exhausted. As all our flies were reared on meat, the larvae cannot be strictly classified as carnivorous or parasitic; they should therefore be regarded as facultative carnivores.

For the study of the sexual ratio of their progeny, observations were made both with laboratory-bred and wild females, and the data obtained have been entered in Tables I and II. The fact that all members of a single batch of offspring of a female, whether it was caught in nature or bred out in the laboratory, belonged to one sex is extremely interesting, and has not hitherto been reported, as far as we are aware, in any other insect where the method of reproduction is by mating.

Table I. *Laboratory-reared females*

		No. of 1st stage larvae counted	No. of adults bred out	Percentage bred out	Sex of progeny
No. 1	1st batch	153	85	55·5	Females
	2nd batch	195	186	95·3	,,
	3rd batch	49	22	55·1	,,
No. 2	1st batch	239	311*	60·7	,,
	2nd batch	221			
No. 3	1st batch	122	98	80·3	Males
	2nd batch	213	167	79·3	,,
No. 4	One batch	?	82	—	,,
No. 5	One batch	?	113	—	,,
No. 6	One batch	?	91	—	,,
No. 7	One batch	237	173	72·9	,,
No. 8	One batch	204	134	65·6	Females
No. 9	One batch	229	164	71·6	Males

* These two batches of larvae from this female were not separated.

Table II. *Wild females*

		No. of 1st stage larvae counted	No. of adults adults bred	Percentage bred out	Sex of progeny
No. 1	One batch	108	45*	—	Males
No. 2	One batch	86	86	100	Females
No. 3	1st batch	163	118†	72·3	,,
	2nd batch	191	181	94·7	,,
No. 4	One batch	106	99	93·3	Males
No. 5	One batch	190	184	96·8	,,

* This was the first batch reared of which sixty larvae and pupae were killed.

† Many escaped: some were captured and they were all identified as females.

In view of the fact just mentioned that the offspring of *Chrysomyia rufifacies* are unisexual, it would certainly be interesting to show the results of experimental matings which we carried out, where one male was allowed to mate with three females, say X, Y, and Z. The progeny of X and Y comprised only males and that of Z only females (Fig. 1, Exp. 3). When a small number of females were kept in contact with a larger number of males, the progeny in such cases also comprised unisexual members (Fig. 1, Exp. 4). We have already pointed out that a single mating is capable of producing at least three batches of eggs and perhaps more. The successive batches of eggs deposited by an individual female always produced the same sex as the first. One or more batches of males only or of females only were thus obtained from a single female (Fig. 1, Exps. 1–5).

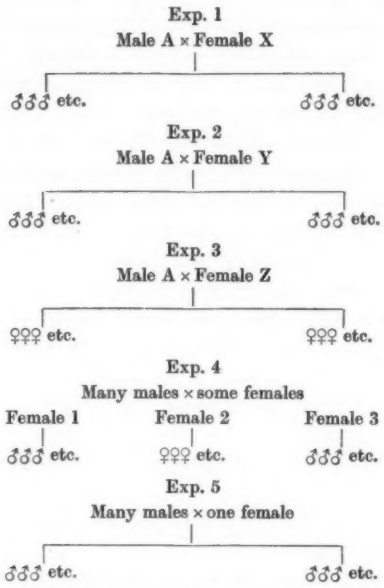

Fig. 1. Mating experiments with *C. rufifacies*.

Discussion

It will be evident from Tables I and II that out of nineteen batches of larvae, no single instance was encountered where the progeny comprised members of both sexes as commonly occurs in insects. Any explanation to suggest the occurrence of unisexual progeny on account of a heavy selective mortality in earlier stages cannot be reasonably accepted.

In the paper on the bionomics of blow-flies of sheep in Australia, *Lucilia cuprina*, *L. sericata*, *Chrysomyia rufifacies*, *Calliphora stygia* and *C. augur*,

Mackerras (1933) has given a short account of the sex ratio of the progeny, but there is no mention of any abnormality such as we have encountered. It must be presumed that either the Australian variety of *rufifacies* behaves differently or the phenomenon was overlooked, as the flies were bred out in large numbers in an insectary.

The occurrence of unisexual progeny with biparental reproduction is, we believe, extremely unusual, if not unique among animals. Confirmation by other workers is therefore desirable.

The nearest approach to this phenomenon seems to be the production of parthenogenetic male-producing and female-producing females in the gall-fly (Cynipidae), *Neuroterus lenticularis* (Doncaster, 1920). The cytological explanation of the parthenogenetically developed generations is well known, but it is not explained why the sexual females have either only male-producing daughters or only female-producing daughters. The case of *Chrysomyia rufifacies* described here has not been cytologically investigated, but it may be said that any cytological explanation, if there is one at all, must account for the fact, elucidated from experimental matings referred to previously, that the progeny of both sexes may be obtained when one male is mated with several females, each female producing only males or only females.

In view of the fact that no true parthenogenesis occurs in *C. rufifacies*, as oviposition is dependent on mating, it becomes difficult to offer any plausible explanation in support of such a phenomenon. Further, one has to consider that the birth of unisexual progeny does not bear any relation either to food or to season, as both parents, males and females, were sustained on the same kind of food and the phenomenon was encountered equally in winter and in summer.

Summary and conclusions

1. Observations on the bionomics of *Chrysomyia rufifacies* Macq. in India have been recorded.

2. Protein is essential for the maturation of eggs, which is complete in about 5 days after emergence.

3. Mating is necessary for oviposition, though egg formation can proceed independently of mating. A single mating is sufficient for at least three batches of eggs.

4. Eggs hatch in 8–12 hr. after they are laid.

5. The average number of eggs produced is 210 (bred flies).

6. The development from egg to adult occupies about $9\frac{1}{2}$ days in summer.

7. The larva is semi-carnivorous, and the floor of the pharynx is provided with ridges.

8. Females of this species produce offspring of one sex only, either all males or all females. This phenomenon, which is independent of diet and of season, is extremely rare among animals especially as parthenogenesis does not occur in this insect.

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A NEW SPECIES OF *CAMALLANUS* FROM THE STOMACH OF *KINOSTERNON HIRTIPES*. IV[1]

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(With 3 Figures in the Text)

Set of seven of these nematodes, two males and five females, taken from a fresh-water tortoise from Tasquillo, State of Hidalgo, Mexico, collected in 1937.

Camallanus parvus n.sp.

Male. Small, measuring 3·783 mm. in length by 0·292 mm. in breadth, with transversal striations in the cuticle. The body presents its maximum width at the level of the anterior oesophagus.

The cephalic extremity is narrower than the broadest part of the body; the buccal capsule has two valves in each of which there are eleven straight ridges, not reaching the ring, and directed at an angle; corresponding to each valve, four whole ridges and a short one. In the middle part, at the level of the middle papilla, there is also a short single ridge. The buccal capsule is 0·107 mm. long by 0·115 mm. wide. The chitinous ring at the base of the capsule is 0·086 mm. in diameter. The external branches of the "trident" are 0·086 mm. long, and the middle one 0·061 mm. long; they are flat and wide.

The anterior oesophagus is 0·328 mm. long and 0·066 mm. wide at the anterior portion and 0·111 mm. wide at the posterior one; the glandular oesophagus is 0·471 mm. long by 0·123 mm. wide. The nervous ring is at 0·172 mm. from the anterior extremity and the cervical papillae 0·273 mm. from the same point. The anus is at 0·092 mm. from the posterior extremity.

The caudal end is provided with two allae; 7 pairs of preanal and lateral papillae with a long peduncle, and 4 pairs of postanal papillae, three of them immediately behind the cloacal opening and a smaller one at the extremity. The caudal allae are 0·273 mm. long. The spicules are very dissimilar, the largest (only one observed) is 0·585 mm. long by 0·016 mm. wide and the hair-like process which starts at the distal extremity of the spicule measures 0·041 mm.

Female. Much more developed than the male, it measures 7·150–7·900 mm. in length by 0·370–0·390 mm. in width; the buccal capsule is 0·115–0·135 mm. long by 0·131 mm. wide; the chitinous ring from the base has a diameter of 0·094–0·098 mm. The lateral branches of the "trident" are 0·090 mm. long and the middle one 0·074 mm.; the anterior oesophagus measures 0·370 mm. in

[1] Fifty-first contribution of the Laboratory of Helminthology of the Institute of Biology of Mexico.

length and 0·082 mm. in width at the anterior portion and 0·131–0·152 mm. in width at the posterior one; the glandular-oesophagus is 0·585 mm. long and 0·131–0·135 mm. wide; the anus opens at 0·253 mm. from the posterior extremity. The posterior extremity is finger-like and ends in three papillae.

The nervous ring is at a distance of 0·173–0·213 mm. from the anterior end. No cephalic papillae could be observed, nor the excretory pore, either.

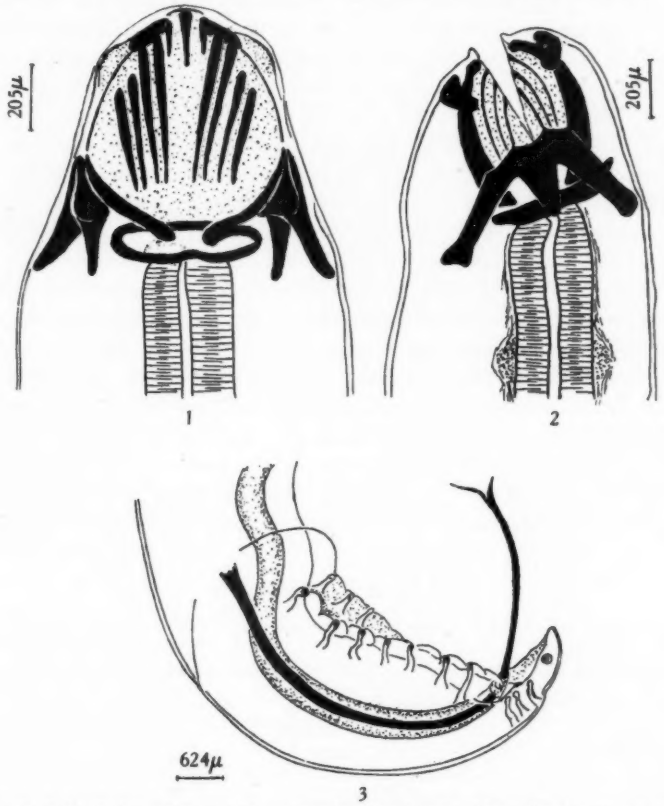

Fig. 1. Lateral view of the anterior extremity of a female of *Camallanus parvus* n.sp.
Fig. 2. Ventral view of the anterior extremity of a male of *Camallanus parvus* n.sp.
Fig. 3. Caudal extremity of male. Lateral view.

The vulva presents greatly developed lips and opens in the posterior end of the body at 3·350–3·800 mm. from this point. The two uteri are opposite each other.

Host. Chinosternum hirtipes.

Localization. Small intestine.

Geographic distribution. Tasquillo, State of Hidalgo, Mexico.

Type. Helminthological Collection of the Institute of Biology, Mexico.

Discussion

Camallanus parvus is similar to *C. scabrae*, but it differs fundamentally from it by the ridges in the buccal capsule, by the number of papillae in the caudal region and by the structure of the spicule at the right.

In each one of the valvae there are eleven straight ridges that do not reach the ring, eight complete, two short and a small medium single one. The number of pairs or preanal papillae is seven; there are no adanal papillae and there are four pairs of postanal papillae. The largest spicule presents a hair-like process in its distal portion, morphologically different from the one in *C. microcephalus* and *C. scabrae*.

In the original description of *C. scabrae* MacCallum makes reference to twelve ridges in each valve of the buccal capsule, four of them being short. Törnquist speaks of seventeen ridges: fourteen complete and bent, two short and a single medium one; besides, the presence of seven pairs of preanal papillae, two adanal and three postanal.

From the analysis of the characters of both species, we see that there is a close relationship between them; however, *C. parvus* has enough proper characters to be considered as a new species.

Few nematodes have so precise and definite characters as those in the genus *Camallanus*: the ridges in the buccal capsule, as to number, distribution and direction; the form of the extremities of the three branches of the "trident" and the caudal papillae with the spicular apparatus, are characters to be taken into consideration when a new species is formed. Therefore, when making a new description, these structures will be described with all details.

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A NEW MITE FROM THE SOUTH AFRICAN PANGOLIN

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(With 6 Figures in the Text)

Some years ago the South African Museum received a tube of mites taken from the South African scaly anteater, *Smutsia temmincki*, by Dr R. Bigalke, Director of the National Zoological Gardens at Pretoria. The tube contained more than 200 well-preserved gamasid mites, and I wish to express my thanks to Dr Bigalke and the authorities of the South African Museum for affording me this opportunity of studying these parasites.

In November 1938, Mr B. Peers, Curator of the Snake Park at Cape Town, presented me with another tube of these mites from the same host. Mr Peer's tube also contained a large number of specimens, and I am furthermore indebted to him for a sketch and some notes which are referred to at the end of this paper. Mr Peer's pangolin, which he was able to keep alive for a week in his snake park, came from the Northern Transvaal. Owing to lack of literature in South Africa, I have been unable to compare these specimens with all of the numerous genera of gamasides that have been described up to the present time. As it cannot be placed among any of the known genera I propose the following new genus for its reception.

Manisicola n.gen.

Body almost entirely covered with a scute which is devoid of large spines; posterior end of body with four to ten long stout spines. Anal shield separated from the other ventral shields in both sexes, armed with three spines.

Mandibles without a spine near the apex of either the fixed or movable digits. Leg I stouter and shorter than the remaining legs, tarsus I not divided, tarsi II–IV divided by a suture. Claws of tarsus I much stouter, shorter, and more curved than those of the remaining tarsi, not connected with the apex of the tarsus by a long slender ambulacral stem as in tarsi II–IV. Patellae and tibiae of legs with some very long sensory setae. Body size large.

Manisicola africana n.sp. (Figs. 1–5)

Male. Dorsal surface (Fig. 1). Body rather elongated and more or less parallel-sided; almost the entire surface covered with a strongly chitinized, semitransparent, reddish-brown scute, only a small projecting subtriangular portion at the posterior end of the body uncovered; this uncovered portion varying considerably in size but always present. Dorsal chitinous scute

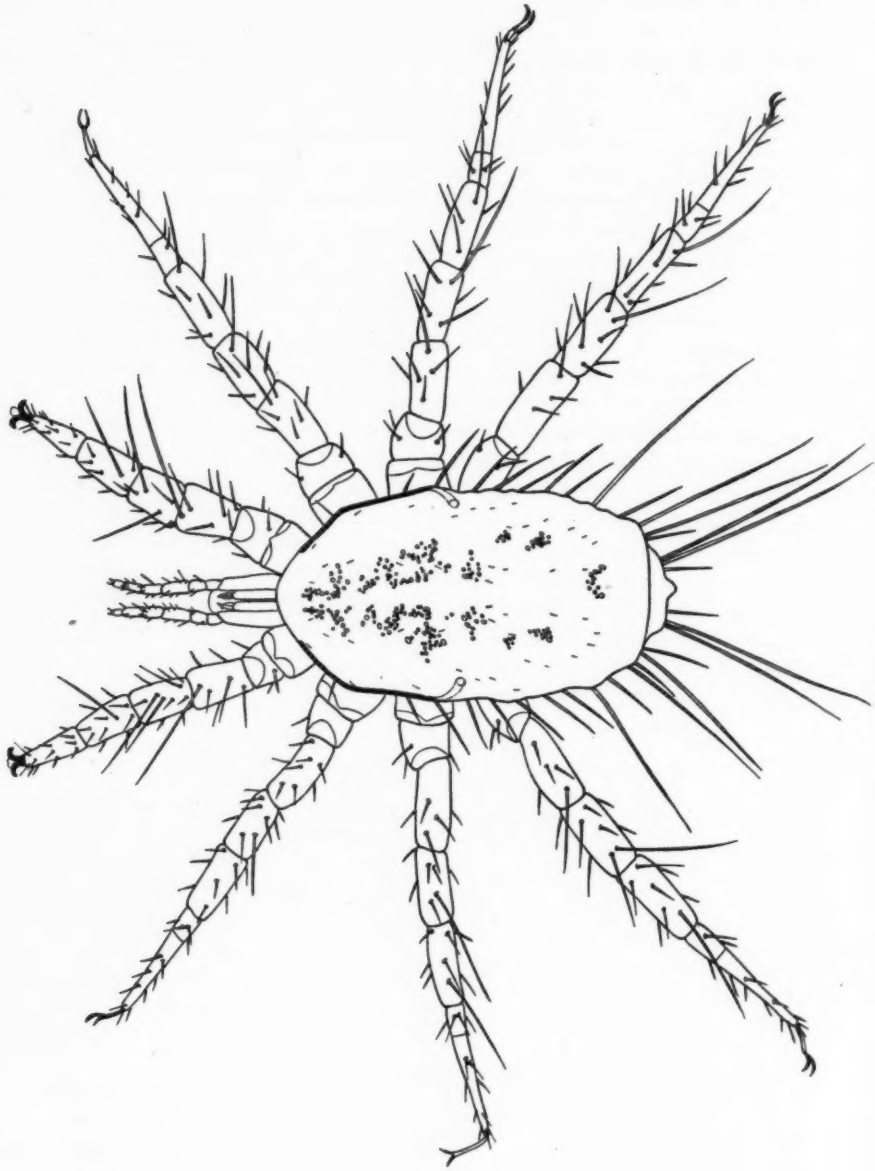

Fig. 1. *Manisicola africana* n.sp. ♂. Dorsal view.

sculptured as in Fig. 1, otherwise quite smooth and shining, unarmed except for a number of minute, symmetrically placed setae. The main tracheal tubes

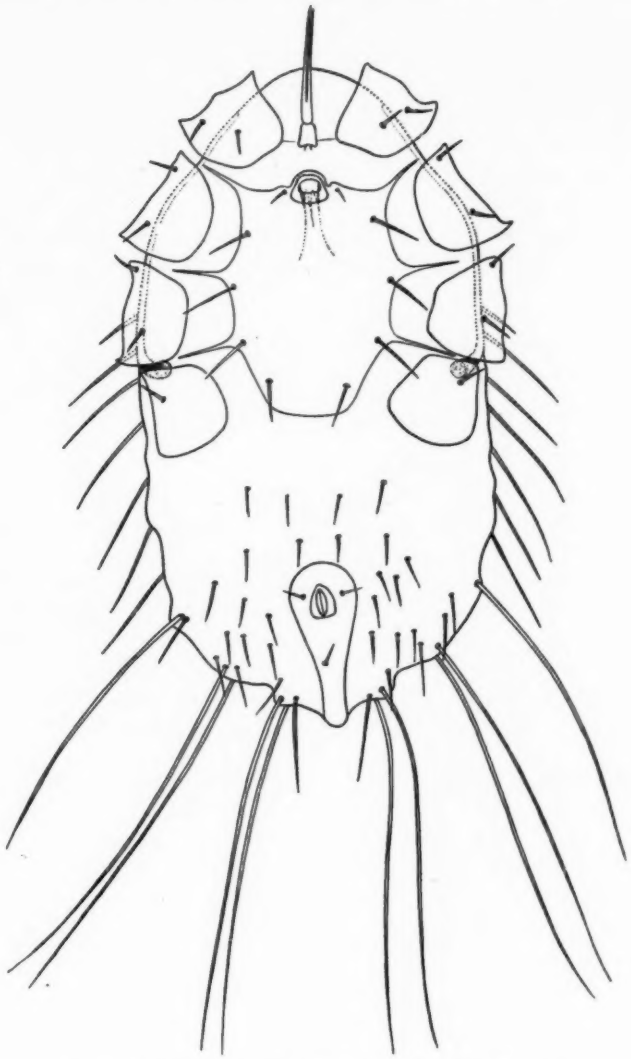

Fig. 2. *Manisicola africana* n.sp. ♂. Ventral surface of body.

running along the dorso-lateral margin of the body for the greater part of their length, the peritremes opening on the ventral surface between coxae III and IV.

Fig. 1. *Manisicola africana* n.sp. ♂. Dorsal view.

Ventral surface (Fig. 2). Ventral shields apparently consisting of only two parts, the large sternal shield, and the anal shield from which it is widely separated. The large sternal shield with long slender projections between the coxae, very clearly defined except along its posterior border, and provided with four pairs of large conspicuous spines and a smaller spine on each side of the genital aperture. Metapodal shields absent. Anal shield much longer than wide, club-shaped, reaching to the posterior apex of the body, and armed with three small spines, the unpaired spine about half-way between the anal aperture and the posterior apex of the shield. Coxae of legs with two short spines on each of I–III, IV with only one spine. Area between the fourth coxae and posterior margin of body with fairly numerous spines as in Fig. 2. Posterior margin of body with ten long setose spines equal to about two-thirds the length of the body, and some other shorter ones, all these inserted at the edge of the postero-lateral margins, or near them on the ventral surface.

Mandibles as in Fig. 5*b* seen from the side.

Pedipalps normal.

Legs. Seen from above (Fig. 1) with the first pair distinctly shorter and stouter than the others; tarsus of leg I almost twice as wide as those of II–IV and not divided by a suture near the base as in the remaining legs; claws of leg I much more thickset, shorter, and more curved than those of legs II–IV, the arrangement and number of the spines near the base of the claws also quite different from that of the remaining tarsi (Fig. 5*d*). At the apex of tarsi II–IV, on the ventral surface, a pair of stout spur-like spines can be seen which are absent in tarsus I (Fig. 5*c*); the ambulacral stem, very long and slender in tarsi II–IV, appears to be quite absent in tarsus I, and the slender claws are provided with an empodium consisting of two delicate, distally expanded hairs which are also not found in the first leg. In general the claws of leg I appear to be modified for attachment, those of the remaining legs for walking purposes.

All segments of the legs well provided with fairly stout spines of variable length, the patellae and tibiae with some much longer and slenderer setiform spines, those of leg II, however, shorter than in the remaining legs. No segments of the legs or pedipalps armed with short spurlike spines of outstanding thickness.

Female. Dorsal surface (Fig. 3). Body shorter and proportionally wider than in the male, more or less oval, and generally a little wider behind than in front. Dorsal surface almost entirely covered with a strong scute similar to that of the males though generally darker in colour, and with the same type of sculptured pattern. Scute smooth and shiny, without large spines but with fairly numerous minute hairlike setae.

Ventral surface (Fig. 4). Sternal shield fairly well defined except at its base, with a pair of lateral spines; genito-ventral shield as in Fig. 4, the junction of the genital and ventral portions rather ill-defined, the ventral portion with a spine adjacent to each lateral margin. Coxae of legs armed

as in the male. Remainder of ventral surface armed with spines more or less as in the male. Posterior margin of body with only four long setose spines and some shorter ones, the long spines both actually and proportionately shorter than those of the male, being about half the length of the body.

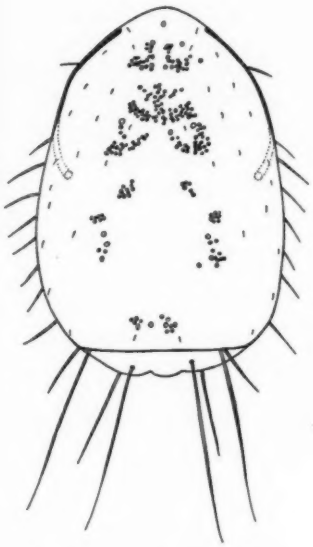

Fig. 3. *Manisicola africana* n.sp. ♀. Dorsal surface of body. Drawn to the same scale as Fig. 1.

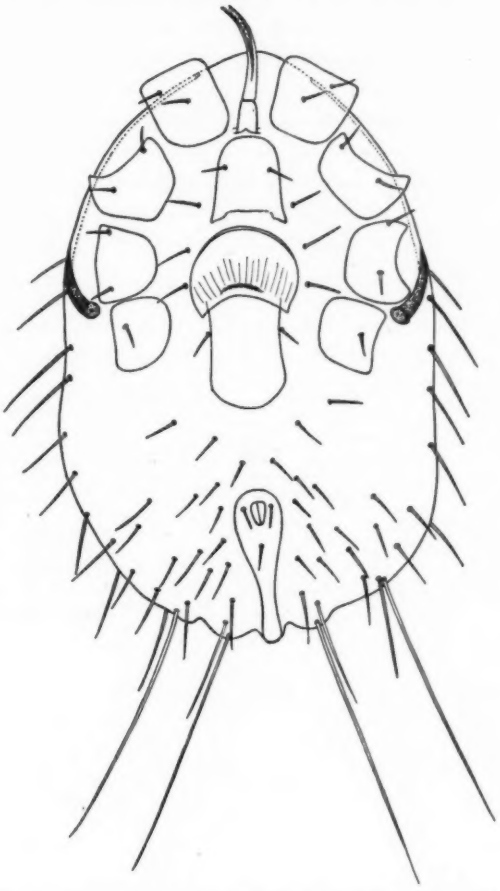

Fig. 4. *Manisicola africana* n.sp. ♀. Ventral surface of body. Drawn to the same scale as Fig. 2.

Mandibles as in Fig. 5*a* seen from the side.

Pedipalps and *legs* armed as in the male.

Dimensions. Male: Average length of body 1870μ; length of body including posterior spines 2910μ; length of body including posterior spines and extended mouthparts 3420μ; width of body 1074μ. *Female:* Average length of body 1518μ; length of body including posterior spines 2240μ; length of body

including posterior spines and extended mouthparts 2573 μ, width of body 1040 μ.

This robust species is remarkable on account of its unusually large size. The sexes can be outwardly distinguished by the shape of the body, that of the male being longer and parallel-sided while in the female it is shorter and proportionately wider, and more oval in shape. The male furthermore has ten long, more or less equal-sized setose spines along the postero-lateral

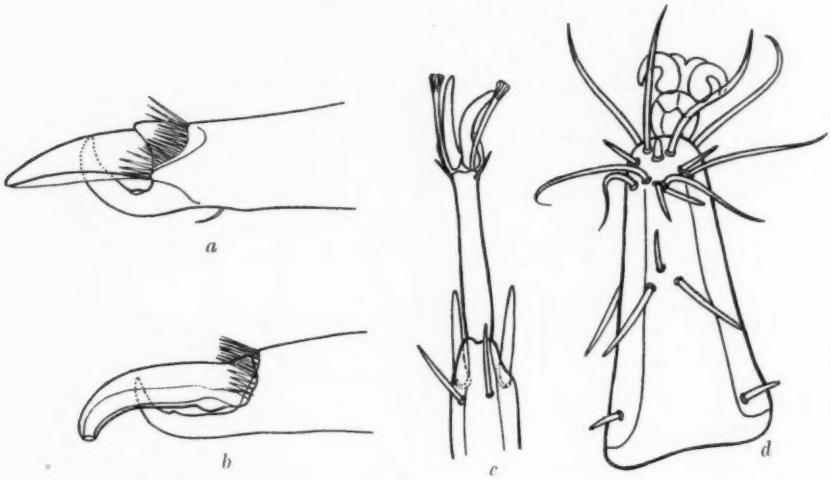

Fig. 5. *Manisicola africana* n.sp. *a*, mandible of ♀; *b*, mandible of ♂; *c*, apex of leg III, dorsal view; *d*, apex of leg I, dorsal view (of a ♂ specimen).

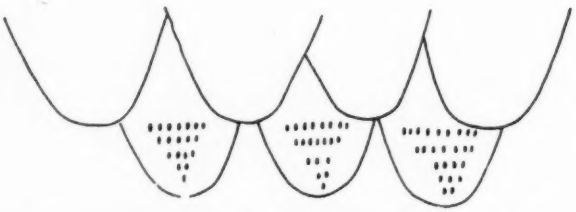

Fig. 6. Diagrammatic sketch of some of the dorsal scales of the pangolin to show the position taken up by the mites.

margin of the body, while the female has only four such spines, which are considerably shorter than those of the male. The dorsal scute seems also to be more strongly chitinized in the female than in the male.

In Dr Bigalke's specimens the proportion of the sexes was almost equal, 42 % of the total being males; in Mr Peer's specimens on the other hand only 10 % were males.

ECOLOGICAL NOTE

I have to thank Mr B. Peers for kindly sending me some observations and a sketch of the living mites on the scales of the host made during the time he kept his pangolin alive at Cape Town. Fig. 6 has been based on this sketch.

Mr Peers says: "When the pangolin was placed in the sun the mites were first noticed; it was as if they sought warmth as well as the host. They ran *sideways* very quickly and took up a definite formation on the *underlying* scales (Fig. 6). This formation while exposed to the warmth of the sun was in full view; when disturbed by the tap of a fingernail on the scutes the mites ran quickly and hid under the *overlying* scales. None of them adhered to the soft skin under the scales; they seemed to live in colonies or batches on certain parts of the animal only."

No larval or nymphal stages were contained in these tubes, though doubtless they would be found on the animal if sought for. In the event of gamasid mites having already been described from pangolins it would be of great interest to compare parasites from the various other host forms living in Central Africa, Java and India, with the species under consideration.

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CERCARIA STRIGATA LEBOUR FROM *CARDIUM EDULE* AND *TELLINA TENUIS*

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(With 1 Figure in the Text)

Cercaria strigata was first named and described briefly by Lebour (1908) from *Tellina tenuis* and *Donax vittatus* at Alnmouth, Northumberland. It was recorded again by the same author (1911) in 3% of *Tellina tenuis* at Millport. What was almost certainly the same cercaria had been previously noted by Giard (1907) between the mantle and shell in the same hosts. Giard did not name or describe the cercaria but suggested that it was the young stage of *Gymnophallus oedemiae* (Jameson) (=*G. somateriae* (Levins)) from the scoter *Oedemia nigra* L.

As will be shown later, *Tellina tenuis* and *Donax vittatus* are the second intermediate hosts of this form which is therefore the metacercaria stage. The first intermediate host has not previously been known, but the writer has now found the sporocysts to occur in *Cardium edule*. An account of these, and a complete description of the anatomy of the metacercaria, are given below.

The metacercaria was found at Millport in 1937 in *Tellina tenuis* from Kames Bay, occurring in 105, or 70%, of the 150 specimens examined. Since then it has been met with at varying times in the Dovey Estuary where the percentage infection during 1938 was 42. More recently, in June 1939, the degree of infestation seems to have risen, every specimen of 52 examined containing the parasite. The metacercaria occurs between the mantle and the shell at a point about one-third of the distance from the umbo to the gape and about midway along the side of the body. This position was constant in every specimen examined, the parasites occurring singly or in a group of from one to five either on one side or on both sides of the body. They are attached to the mantle by both suckers and apparently remain stationary in a contracted condition. They are not embedded in the mantle as is the muscle metacercaria of Jameson (1902), but come away quite readily when the shell is removed in sea water and crawl about on the bottom of the watch glass. For investigating the anatomy, specimens so obtained were examined alive between slide and cover glass. All measurements were made from living material and are as follows:

	Expanded mm.	Contracted mm.
Length	0·40	0·17
Breadth	0·095	0·30
	mm.	
Oral sucker	0·09 × 0·075	
Ventral sucker	0·05 × 0·048	
Pharynx	0·025 × 0·021	
Testes	0·05 × 0·024	
Ovary	0·03 × 0·02	

The body of the metacercaria is broadly ovate in outline and tapers slightly to the posterior extremity. The delicate cuticle covering the surface is armed with transverse rows of conspicuous spines which decrease slightly in size posteriorly. Immediately surrounding the mouth is a narrow area devoid of spines on the margin of which, on the dorsal side, open the ducts of the penetration gland cells. There are two suckers, the oral being almost twice the diameter of the ventral; the ratio between them is 9 : 5. The alimentary canal consists of a muscular pharynx contiguous with the oral sucker, followed by a short oesophagus which bifurcates into two intestinal caeca extending as far as the anterior border of the ventral sucker. The caeca are large and rounded and capable of distension and contraction. When fully distended, they are hollow thin walled sacs and when contracted the lining layer is pushed into the cavity in a number of finger-shaped projections which obliterate it almost completely. The caeca are devoid of contents, unlike Jameson's (1902) metacercaria from *Mytilus* where they are distended with yellowish granular material. A large number of penetration gland cells occurs at the anterior extremity around the oral sucker. They are unicellular with ducts opening by a series of pores along the dorsal border of the mouth at the outer limit of the spineless area. These glands are probably histolytic in function, and enable the cercaria to bore its way out of the digestive gland of its first intermediate host, and also to bore through to the outside of the mantle in its second intermediate host. The excretory system includes a conspicuous excretory vesicle lying dorsally, and described by Lebour (1908) as lyre-shaped. This is the only part of the excretory system so far known. It opens by a pore at the posterior end. Anteriorly, it extends on either side of the oral sucker and is figured by Lebour as ending in a single blind diverticulum on each side. In the present specimens the anterior extremity of each lateral arm is bifurcated as far back as the posterior border of the oral sucker. This feature is constant in all the specimens examined, and it was thought at first that this possibly was a different species from that described by Lebour, but as the dimensions of the body and the form of the alimentary canal agree it was assumed to be the same. Other constant features of the excretory bladder are two lobes on either side near the excretory pore, and a ventral lobe lying below the intestinal caecum on each side. This latter, though always present, varies in prominence with the expansion or contraction of the body. The excretory vesicle is filled throughout its length with excretory granules. There are eight flame cells on each side arranged according to the formula $2\,[(2+2)+(2+2)]=16$. Their positions are illustrated in the figure. The ducts from the flame cells were very difficult to trace owing to the density of the excretory vesicle, but an examination of a very large number of specimens with the right amount of pressure on the cover glass enabled the whole system to be followed. The flame cell capillaries, four anteriorly and four posteriorly, unite into ducts which run respectively backwards and forwards to join one another at the level of the anterior border of the ventral sucker, where they form a main lateral excretory duct which runs

forwards to open into the excretory vesicle on the ventral side at the root of the ventral lobe. The main lateral excretory duct has tufts of vibratile cilia along its length and pursues the looped course illustrated in the figure. The whole flame cell system lies ventral to the excretory vesicle. Rudiments of the genital system are present in the form of two oval obliquely placed testes situated one

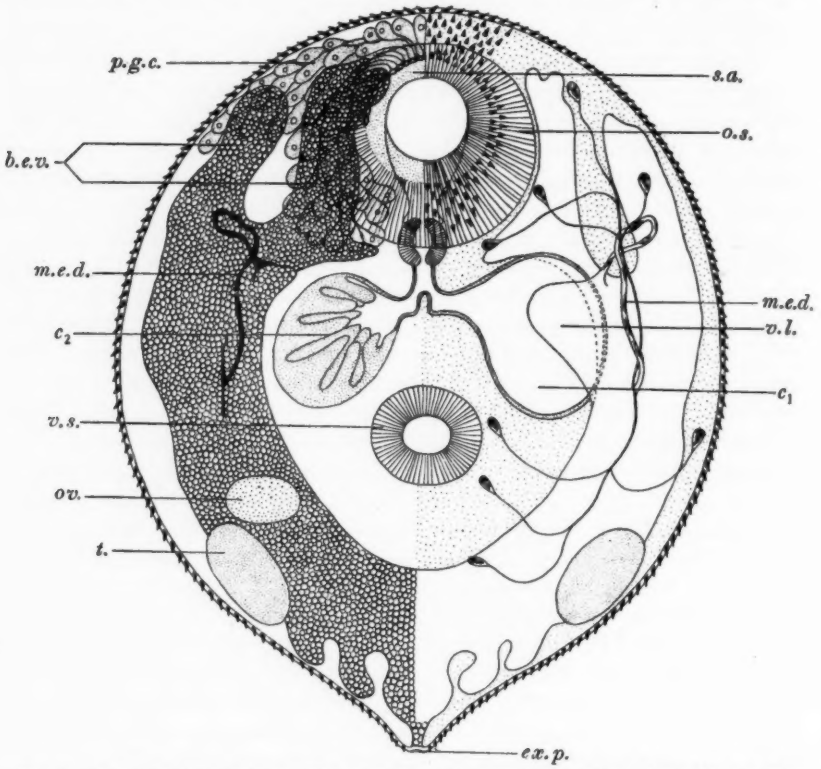

Fig. 1. *Cercaria strigata* Lebour. The excretory system and penetration gland cells are fully illustrated on one side only. The intestinal caeca are shown in the expanded state on one side, and the contracted state on the other. *b.e.v.* bifurcated anterior end of excretory vesicle; c_1, caecum expanded; c_2, caecum contracted; *ex.p.* excretory pore; *m.e.d.* main excretory duct; *o.s.* oral sucker; *ov.* ovary; *p.g.c.* penetration gland cells; *s.a.* spineless area around mouth with openings of penetration gland cells; *t.* testis; *v.l.* ventral lobe of excretory vesicle; *v.s.* ventral sucker.

on either side ventral to the excretory vesicle and about half-way between the ventral sucker and the posterior extremity, and a transversely oval ovary just in front of the right testis.

The only suggestion which has so far been made concerning the other larval stage of this trematode is that of Pelseneer (1906) who considered it to be the young form of his fork-tailed *Cercaria syndosmyae*. This seemed highly im-

probable as *C. strigata* is undoubtedly the larval stage of a species of *Gymnophallus* and no tailed forms of *Gymnophallus* larvae are known. Also, the two suckers in *Cercaria syndosmyae* are equal in size, whereas in *C. strigata* the oral is almost twice the diameter of the ventral. This suggestion, therefore, was dismissed, and it was decided to make a search for the first intermediate host. *Tellina tenuis* itself was examined for sporocysts, but dissection and serial sections gave negative results. Attention was then directed to the other molluscs in the same area. Immediately associated with *T. tenuis* in the Dovey Estuary are *Cardium edule* and *Macoma balthica*. *Scrobicularia plana* and *Mytilus edulis* occur some distance away, and *Littorina littorea* and *Peringea ulvae* are found on the surface of the sand a little higher up the shore. From this distribution it seemed that the most likely intermediate host would be either *Cardium edule* or *Macoma balthica*, and examination of these two species proved that the former was the first intermediate host of *Cercaria strigata*. The sporocysts occur deep down in the digestive gland. They are thin-walled colourless oval structures filled with cercariae in various stages of development. There is no contained brown granular material as described by Cole (1938) for the sporocysts of *C. cambrensis* from the same host. Cercariae removed from the sporocysts show the same structure as the metacercaria, the bifurcated ends of the excretory vesicle being a valuable diagnostic feature. Two other *Gymnophallus* cercariae have been described from *Cardium edule*, namely *C. margaritae* Jameson and *C. cambrensis* Cole. *C. strigata* can be distinguished from the former by the absence of eye spots and sensory bristles, and by the position of the sporocysts, which in *C. margaritae* are immediately under the hinge line, and from the latter again by the position of the sporocysts which are thick-walled and contain brown granular contents. The measurements, and the ratio between oral and ventral suckers, are different in each case, and the form of the excretory vesicle in *C. strigata* is quite characteristic. *C. cambrensis* is the young stage of the mussel metacercaria and of *Gymnophallus margaritarum* (Dubois). *Cercaria margaritae* probably also has a metacercaria stage in the mussel.

As already remarked, the adult stage of *Cercaria strigata* is doubtless a species of *Gymnophallus* inhabiting a bird. Giard (1907) suggested *G. oedemiae* (Jameson), but there are some conspicuous differences in structure which make this unlikely. Of the several species of *Gymnophallus* described, the most likely adult form of *Cercaria strigata* is *Gymnophallus macroporus* Jameson and Nicoll from *Oedemia nigra*, or even more likely still *Gymnophallus deliciosus* (Olss.) from *Larus argentatus*, *L. fuscus*, and *L. canis*. Lebour (1908) suggested that this might be so, and an examination of large numbers of marine birds on the Cardiganshire coast has revealed only this species of *Gymnophallus* from the gall bladder of *Larus argentatus*. *Oedemia nigra* is rare and it was not possible to obtain any specimens. The measurements of *Cercaria strigata* and *Gymnophallus deliciosus* are given below. They seem to agree very closely except, of course, that the adult worm is about three times the size of the larva. The ratio

between the suckers is about the same, and the position of the testes and ovary. In all the other described species of *Gymnophallus* the gonads are more or less on a level with the ventral sucker instead of being behind it.

	Cercaria strigata	*Gymnophallus deliciosus*
	mm.	mm.
Length	0·40–0·17	1·10–2·30
Breadth	0·09–0·30	0·50–0·75
Oral sucker	0·09	0·20–0·25
Ventral sucker	0·05	0·16–0·20
Pharynx	0·025	0·06

This suggestion needs experimental evidence before it can be accepted.

During the examination of the molluscan fauna of the Dovey Estuary several other species of larval trematodes have been found. They are *Cercaria cambrensis* Cole, and *Bucephalus haemeanus* Lacaze-Duthiers from *Cardium edule*, *Cercaria lophocerca* Lebour and *C. ephemera* Lebour from *Peringea ulvae*, *Cercaria linearis* Lespés and *C. lophocerca* Fil. from *Littorina littorea*, and the encysted stage of *Cercaria* (*Echinostomum*) *secundum* Nicoll from the foot of *Mytilus* and as not recorded before from the foot of *Macoma balthica*. In addition, two parasitic Rhabdocoeles belonging to the family Graffillidae occur, namely *Paravortex cardii* (Hallez) in *Cardium edule*, and *Graffilla gemellipara* Linton in *Scrobicularia plana*. These are the only parasitic Rhabdocoeles so far recorded for this country. Chrenko found *Paravortex cardii* in the ovary of *Cardium edule* at Plymouth in 1934. It is an easily recognizable species, swimming in circles. *Graffilla gemellipara* was first recorded by Linton (1910) from *Modiolus plicatulus* in America. Leigh Sharpe (1933) found it at Plymouth in *Cardium edule*, and Chrenko repeated this observation a year later. In the Dovey Estuary it has not been found to occur in *Cardium*, but in the digestive gland and gonad of *Scrobicularia plana*. It is very common, occurring in almost every specimen examined, and is easily recognized by its transparent body containing about eight spherical cysts each with two ciliated young. Both parent and young are provided with two bean-shaped eye spots. What Nicoll (1906) described as a "ciliated sporocyst" from *Cardium edule* at St Andrews is undoubtedly this Rhabdocoele. His figure and description of it agree with Linton's description of *Graffilla gemellipara*. The fact that it does not occur in *Cardium edule* in the Dovey Estuary is strange, but the heavy infection in *Scrobicularia plana* seems to indicate that it prefers this host.

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HERSILIODES PELSENEERI CANU, A PARASITIC COPEPOD OF *LEIOCHONE*

By W. HAROLD LEIGH-SHARPE, M.Sc. (Lond.)

(With 4 Figures in the Text)

Habitat and record. A single female was taken on *Leiochone* sp. by Alan Fisk on 23. viii. 1938 at Roscoff, France.

Body. The body, which was bright pink, is divided into (Fig. 1):

(*a*) A *cephalothorax* which consists of the cephalon and the first or maxillipedal segment, and the first thoracic segment;

(*b*) A *metasome* of three free thoracic segments bearing pereiopods two, three and four;

(*c*) A *urosome* of the sixth and seventh thoracic segments and an abdomen of three segments. The movable articulation is between the fifth and sixth thoracic segments. The sixth and seventh segments are not fused. The sixth segment bears the fifth pair of pereiopods. The seventh segment is broad anteriorly being produced into rounded lobes bearing backwardly-directed, transparent, thorn-like processes as in *Hippomolgus*, posterior to which are the vestiges of the sixth pair of pereiopods immediately posterior to the genital apertures (Fig. 4).

The abdomen is tapering and the first segment at its broadest part is half the width of the metasome at its broadest part. The abdominal appendages are long and tapering, four times as long as wide, with a proximal dilation on the inner margin, and terminating in two long setae of unequal length and one outer shorter one (Fig. 4).

There is a well-marked rostrum.

Appendages (Fig. 2). *Antennules* six-articled, setose. The proximal article small and broad adjacent to the rostrum, the next two articles large and long; the three distal articles elongate but small, the most distal terminating in two long and one short setae.

Antennae five-articled. A plain transversely-directed proximal article with a long seta on the medial border reaching to the upper lip, the other articles reflected upon this. The next article the broadest. The third article terminates in a hook and three long setae; the fourth article articulates with this one in a more dorsal plane; the distal article terminates in three long setae. (Or another interpretation is that the antenna is biramose, the exopodite, which is two-articled, being attached to the endopodite which is one-articled.)

Mandibles, styliform with a separate article distally, and an enlarged base.

First maxillae biramose: exopodite with four long setae, endopodite one-articled with three long terminal setae.

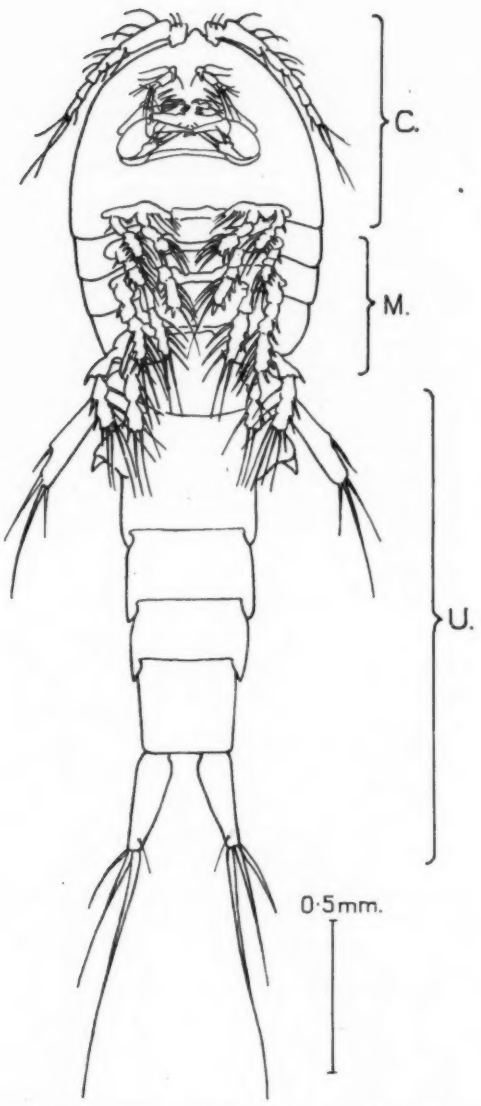

Fig. 1. *Hersiliodes pelseneeri* ♀. The entire animal in ventral aspect. *C.* = cephalothorax; *M.* = metasome; *U.* = urosome.

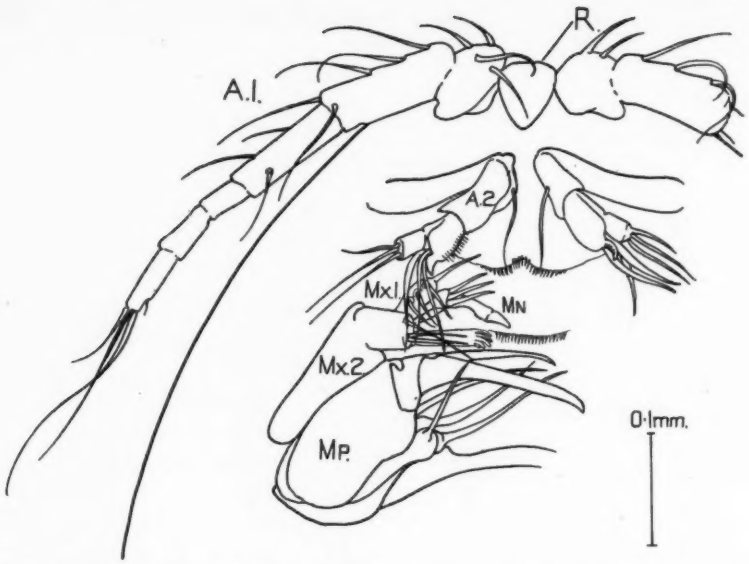

Fig. 2. *Hersiliodes pelseneeri* ♀. Part of the cephalothorax. *R.* = rostrum; *A.* 1 = antennule; *A.* 2 = antenna; *Mn.* = mandible; *Mx.* 1 = first maxilla; *Mx.* 2 = second maxilla; *Mp.* = maxillipede.

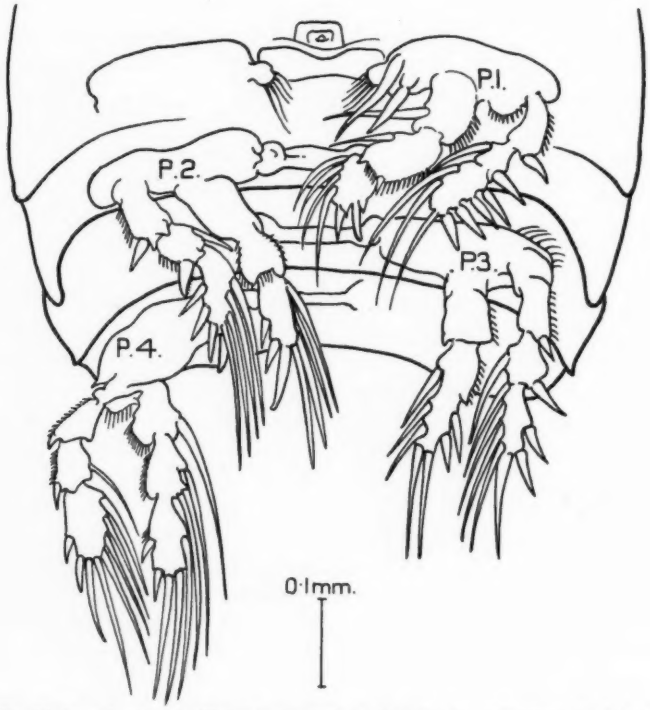

Fig. 3. *Hersiliodes pelseneeri* ♀. Thoracic segments including the metasome. *P.* 1–4 = the first four pereiopods.

Second maxillae two-articled ending in a bunch of straight setae.

Maxillipedes two-articled. The proximal article stout with a number of large setae on its inner margin. The distal article ends in two large setae which are curved and claw-like. This appendage resembles that of *Clausidium*.

The four pairs of *pereiopods* are biramose and three-articled (Fig. 3). In the first pair the endopodite is larger than the exopodite and the protopodite bears on its inner projection two large plumose natatory setae. In the other pairs the exopodite and endopodite are of equal size.

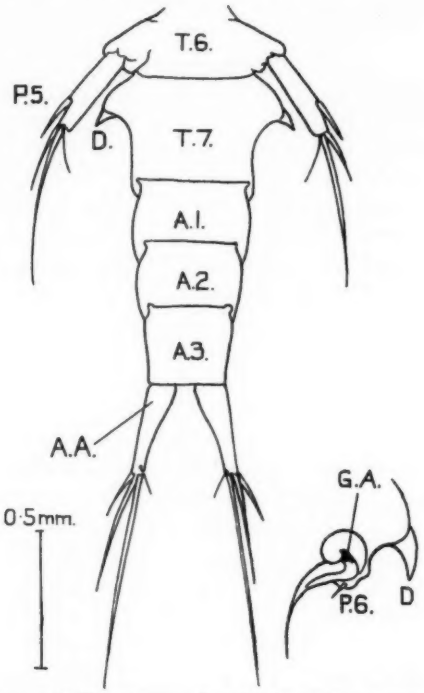

Fig. 4. *Hersiliodes pelseneeri* ♀. The urosome. *T.* 6–7 = the sixth and seventh thoracic segments; *P.* 5–6 = the fifth and sixth pereiopods; *A.* 1–3 = abdominal segments; *A.A.* = abdominal appendages; *G.A.* = genital aperture; *D.* = thorn-like process.

The fifth pair of pereiopods (Fig. 4) are uniramose and one-articled. The article is elongated, three and a half times as long as broad, bears one large subapical seta on its outer edge, terminates in one large and two smaller setae and fits into a socket on the sixth segment. The sixth pair is reduced to a rounded prominence bearing a minute seta.

Generic characters. Urosome half as wide as metasome. Antennules six-articled. Antennae five-articled. The exopodite of the first maxilla bears four long setae. The second maxilla bears a bunch of setae. The distal article of the maxillipede ends in two long setae which are curved and claw-like. In the

first pereiopods the endopodite is larger than the exopodite and the protopodite bears on its inner projection two large plumose natatory setae. The fifth pereiopods are one-articled, elongated, three and a half times as long as broad. The abdominal appendages are elongated, tapering, four times as long as wide, with a proximal dilation on the inner margin, and terminate in two long setae of unequal length and one shorter one. The genital segment has lateral expansions with recurved hooks.

The figures are all drawn with the camera lucida.

The specimen, mounted in balsam, is deposited in the British Museum.

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A NOTE UPON THE SYSTEMATIC POSITION OF "*TRICHOMONAS*" *KEILINI* (BISHOP, 1935)

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In 1935 I described a free-living flagellate, which bore a striking resemblance to the genus *Trichomonas*, and was obtained, on four different occasions during a period of 12 months, from a pond in Lincolnshire. This flagellate has three anterior flagella, and a short marginal flagellum bordering an undulating membrane but without a freely-projecting end. There is no basal fibre at the base of the short membrane. The three free flagella and the marginal flagellum arise from a blepharoplast which lies in front of the single, anteriorly placed nucleus. There is a cystostome. An axostyle frequently is absent, but when present it is slender and siderophilic. Division is similar to that of *Trichomonas hominis* and *T. batrachorum* (Bishop, 1931).

This flagellate from the pond differs from the genus *Trichomonas* in the absence of a basal fibre and in the frequent absence of an axostyle. I hesitated, however, at that time, to create a new genus for it and placed it (Bishop, 1935) tentatively in the genus *Trichomonas*, calling it provisionally "*Trichomonas*" *keilini*. That this was a temporary measure pending further study I emphasized in my paper. Further observations (Bishop, 1936) proved that this flagellate was a free-living form living in the pond, and not merely a parasite present in an encysted state and awaiting suitable conditions to become active.

Lavier (1936) has since published an account of a flagellate discovered by him in stagnant water from two different localities in France. He considered this flagellate to be similar in structure to "*Trichomonas*" *keilini* and his description and figures support this view. On the grounds that a basal fibre (=costa, =côte) is lacking and that he has found individuals in which the marginal flagellum had become free from the undulating membrane, he decides to include "*Trichomonas*" *keilini* in the genus *Eutrichomastix*. Later Hollande (1939) refers to it under this generic name.

If we consider the history of the genus *Eutrichomastix* we find that the generic name *Trichomastix* was created by Blochmann in 1884 for a flagellate, *Trichomastix lacertae*, which had four flagella, one directed posteriorly and three anteriorly. The posteriorly directed flagellum was without an undulating membrane, and a basal fibre was neither described nor shown in the figures. Prowazek's description of this species was similar (Prowazek, 1904). In *Trichomastix serpentis* from *Boa constrictor*, Dobell (1907) describes three

anteriorly directed flagella and one directed backwards. As a result of degenerative changes he found that the posterior flagellum, which normally is free, showed a tendency to adhere to the body, a delicate membrane uniting them. Dobell (1909) found the arrangement of the flagella of *Trichomastix batrachorum* to be similar to that of *T. lacertae*, and he distinguished between *Trichomonas batrachorum* and *Trichomastix batrachorum* by the presence in the former species of an undulating membrane uniting the posterior flagellum to the body. His figures (Plate II) show a basal fibre in *Trichomonas batrachorum* but none in *Trichomastix batrachorum*.

As Stiles (1902), whilst accepting *Trichomastix lacertae* as the type species, had pointed out that the generic name had been given by Vollenhoven[1] in 1878 to a Hymenopteron, Kofoid & Swezy (1915) introduced the generic name *Eutrichomastix* for these flagellates. Kofoid & Swezy agree with Dobell (1907) in describing *E. serpentis* as having three anteriorly directed flagella and a trailing flagellum and lacking a basal fibre.

Evidence upon the relationship of *Eutrichomastix* to *Trichomonas* has been reviewed by me previously (Bishop, 1931). Of particular interest are observations by Chatton and by Grassé. Chatton (1920) found that in cultures of *Trichomonas* from the guinea-pig the flagellum bordering the undulating membrane became free and gave rise to a *Eutrichomastix* form. Grassé (1926) obtained similar results when *T. colubrorum* was subjected to a slightly hypotonic Ringer solution of *p*H 7·5–8. He believes that the two genera should be fused. During the last 19 years many species of *Trichomonas* have been cultivated, in various media, by many workers, but I have found no reference to the appearance of *Eutrichomastix* forms in them. With a view to throwing further light upon the problem Das Gupta (1936) cultivated *Trichomonas* from the grass snake and studied it for 10 weeks without finding in it any tendency to assume *Eutrichomastix* forms. In stained preparations from a pure line of *Trichomonas* from the Boa he found occasional forms in which the marginal flagellum had become detached from the undulating membrane. He never observed such forms in fresh preparations and believes them to be accidental and artificial. A basal fibre was not detected in this strain. He also made repeated examinations of cultures of *Eutrichomastix* from the krait, grass snake, and from *Chaemaeleon quilensis* but the flagellates remained true to the *Eutrichomastix* type. In a strain of *Trichomonas* from the Corais snake, in which he was unable to find a basal fibre, Das Gupta (1936*a*) found that the marginal flagellum occasionally became detached from the undulating membrane. This detachment he considers was probably caused by the pressure in preparing the film. From his experience of *Eutrichomastix* and members of the Trichomonadinae in termites Kirby (1931) does not believe *Eutrichomastix* to be

[1] Mr Clifford Dobell has called my attention to the mistakes in spelling in references to this author's name. The name of the Dutch entomologist who proposed the name *Trichomastix* for a hymenopteron was S. C. Snellen van Vollenhoven—not Vollenhoeven (Kofoid & Swezy, 1915), nor Vollenhoevan (Wenyon, 1926).

a stage in development of *Trichomonas*; but he regards them as separate genera.

During the last 12 years I myself have cultivated *Trichomonas hominis*, *Trichomonas* sp. from *Macacus nemestrinus* and many strains of *Trichomonas batrachorum* for long periods but have never found *Eutrichomastix* forms.

The strain of "*Trichomonas*" *keilini* which I isolated on 10. viii. 34 is still growing luxuriantly, in a medium consisting of an inspissated horse-serum slope covered with inactivated horse-serum 1 : 10 in 0·5% NaCl solution, a little solid, sterile rice being added to each tube before inoculation. From time to time I have examined these cultures, and have once again examined a large number of the living flagellates carefully. In each individual I have found an undulating membrane at the anterior end of the body, extending in some individuals about half way towards the posterior end whereas in others it is very short. I have never found individuals in which the marginal flagellum is free.

My original description was of a flagellate possessing a marginal flagellum united to the body by an undulating membrane which did not reach to the posterior end of the body. This is the type which had persisted in my cultures for five years. The appearance, in a different strain, as observed by Lavier, of some forms devoid of undulating membrane and with the "marginal" flagellum free does not, in my opinion, place the flagellate in the genus *Eutrichomastix*. If the genus *Eutrichomastix* is to be regarded as a separate genus it is the generic name of flagellates of which the predominant form possesses no undulating membrane, in which the posteriorly directed flagellum is therefore free, and in which a basal fibre does not occur. If however, *Eutrichomastix* forms are to be regarded as developmental stages in *Trichomonas*, or as occurring in this genus as the result of physiological or physical changes in the environment, then the generic name *Eutrichomastix* Kofoid & Swezy, 1915 becomes a synonym of *Trichomonas* Donné, 1836.

The flagellate from the pond possesses several characters which, collectively, seem to justify the creation of a new genus. It differs from the trichomonads described hitherto in its free-living mode of life, in the absence of a basal fibre, in the frequent absence of an axostyle, and from the majority of trichomonads, though not from *T. vaginalis*, in the shortness of the marginal flagellum which lacks a free terminal portion. It differs from *Protrichomonas*, created by Alexeieff (1911) for the flagellate found by him in *Box boops* (1910), in that it possesses a marginal flagellum and undulating membrane, both of which are absent in *Protrichomonas*. A basal fibre is absent in both genera. "*Trichomonas*" *keilini* differs from *Coelotrichomastix* Hollande, 1939 in the structure of the axostyle, which is massive and ribbon-like in the latter genus, whilst in the former, when present, it is slender and siderophilic. *Coelotrichomastix* possesses a deep ventral groove not present in "*T.*" *keilini*, although in both genera a basal fibre is absent.

In the genus *Coelotrichomastix* Hollande includes *Trichomastix salina*

described by Entz (1901) from inland, saline water. Although Entz places this flagellate in the genus *Trichomastix* (= *Eutrichomastix*) the arrangement of the fourth, backwardly-directed flagellum as shown in his figures (p. 116, A and B) and the description of its attachment to the body, does not support his classification. Though he does not mention an undulating membrane his description implies the presence of one reaching to the posterior end of the body. The absence of precise details of finer structure makes classification difficult, but, on account of the convexity of the dorsal surface and the presence of a ventral groove, Hollande includes it in the new genus *Coelotrichomastix*.

On account of the superficial resemblance of the flagellate from the pond to *Trichomonas* I propose to create the new generic name *Pseudotrichomonas* for this free-living flagellate. Thus the flagellate formerly named by me "*Trichomonas*" *keilini* becomes *Pseudotrichomonas keilini*. This new genus contains, at present, this single species.

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TECHNIQUE FOR THE ESTIMATION OF PASTURE INFESTATION BY STRONGYLOID LARVAE

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(With one Figure in the Text)

During the investigations that have been carried out at this Laboratory into the factors concerning the development of the strongyloid diseases of grazing animals the requirement has been felt for some method whereby the infective larvae of the parasitic worms could be recovered from the pasture herbage and an estimate made of the relative extent of infection, or possibly, of the actual number of larvae available to the grazing animal.

One of the problems in working out this technique has been that of dealing with a sufficiently large-sized sample of herbage and of separating the larvae from a large amount of debris. It is felt that the new modification of the Baermann Technique that is here described has provided a satisfactory solution of this problem; but another problem, that of the separation of parasitic larvae by biological means from free-living nematodes and their larvae has not been so satisfactorily solved. On finding that the special technique above referred to could readily be used for the separation of trichostrongylid from *Strongyloides*[1] larvae it was hoped to be able to adapt its use to their separation from free-living nematodes but these worms were found to be less easily killed than is generally supposed and although less resistant in general to dryness, poisonous substances, heat and osmotic tension than are the parasitic larvae, no method was found to kill them that would not at the same time kill a considerable number of the parasitic larvae. Could any reliable method be found of destroying the free-living and not the parasitic larvae, such as the brief drying on filter paper that is sufficient to kill *Strongyloides* larvae but leaves sheathed parasitic larvae unharmed, it would be a simple matter to separate the living from the dead larvae and save a considerable amount of time at the microscope during the course of this work.

[1] If a mixture of Strongyloides and trichostrongyloid larvae is pipetted on to the surface of a piece of filter paper and allowed to dry the Strongyloides larvae are killed but the others not, and when the paper is then floated, larvae side down, on to water in a petri dish the trichostrongylid larvae gradually regain their activity and free themselves from its surface but the dead Strongyloides larvae remain on the paper and can be removed with it leaving only the living trichostrongylid larvae in the water.

A dirty larval suspension can be cleaned, or living trichostrongylid larvae be separated from dead ones in the same way.

The technique here described enables one to arrive at an estimate of the number of larvae per pound of herbage and although, on account of the sampling difficulties it is not possible to avoid a considerable error, particularly where horse-grazing is concerned, the information obtained is sufficiently reliable to warrant the extended employment of the technique as a means of research.

Method of collecting the sample of herbage

The area of pasture to be sampled is traversed in a zigzag manner, halts being made at about one hundred different places and samples of herbage plucked from four different points at each halt. It is advisable first to stride out the course over which the sample is to be collected so that the number of strides between each of the hundred halts may be found before beginning to collect.

In collecting, two or three pinches of grass are plucked at each halt from each of four places, one immediately in front of the toe of the shoe, and three others as far as can conveniently be reached in front and on either side of the

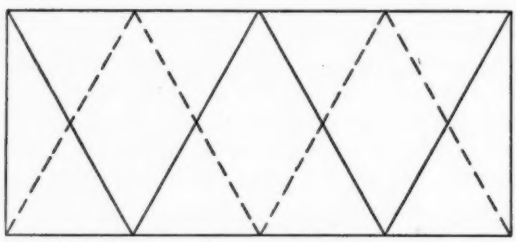

Fig. 1. Track taken by collector A -----. Track taken by collector B ———.

foot; the size of the sample taken from each spot should be approximately the same over the whole field. The grass should be plucked as close to the ground as possible but without pulling up any of the roots as soil interferes with the process of the separation of the larvae.

The plucking of the grass is preferably done with the eyes shut so as to avoid any bias on the part of the sampler in favour of a particular kind of herbage or proximity to deposits of faeces, but on very bare pastures this is not always practicable. About eight ounces is considered to be a suitably sized sample, although from half to twice that size can also be easily handled and gives a satisfactory result.

A second collector takes a separate sample at the same time, not along the same course but beginning at another corner of the field and crossing the course taken by the first collector.

These two separately collected samples each comprising herbage taken from four hundred different spots in the field can then be handled and examined independently to serve as a check on one another.

WASHING THE LARVAE FROM THE HERBAGE

On reaching the laboratory each collector's sample is repeatedly turned over until thoroughly mixed; it is then weighed and is divided into two equal parts by weight. Each of these four parts of two samples is then placed in a large bucket of water to one only of which is added 1000 living and vigorous trichostrongylid larvae and stirred round a few times to ensure their even mixture with the herbage.

After the buckets and grass have been allowed to stand for 2 hr. or so, the grass is taken out by hand and either squeezed or allowed to drain until as much of the washing water as possible runs back into the bucket. Separate pieces of grass may then be removed by scooping through the water several times with a coarse mesh screen and the whole bucketful of washings is then passed through a fine screen of sixty meshes to the linear inch into a clean bucket where it is left to sediment overnight.

SEPARATION OF THE LARVAE FROM THE DEBRIS

The next procedure, carried out on the following morning, is to syphon off the water, leaving the sediment in the bottom of the bucket. This sediment consists of small pieces of living and dead vegetable matter, particles of soil, small soil and herbage animalcules among which are adult and larval free-living nematodes, and the larvae of strongyloid nematodes that are being sought for.

This sediment is then poured into a round-bottomed pint measuring glass and allowed to sediment for about 6 hr. At the end of this period the supernatant water is siphoned off and the muddy sediment containing the larvae is pipetted on to a piece of Whatman No. 1 filter paper of a diameter of 17 cm. standing on several thicknesses of blotting paper. This is done quickly and in such a way that the sediment spreads as evenly as possible over the whole surface. When this process has been completed the preparation is watched very carefully and as soon as the actual shining wetness has disappeared from the surface of the muddy sediment (a matter of seconds only), the filter paper is picked up, in such a way that it can be turned over with the minimum disturbance to the muddy sediment, and gently placed, sediment side down, into a large Baermann's separation apparatus which has been placed in readiness. The only special point about this apparatus is its size, the glass funnel requiring to be large enough to hold a wire screen 19 cm. in diameter and allow the water to rise at least a quarter of an inch above the screen so that the filter paper can be lowered into it without any fear of rubbing the muddy sediment on the surface of the wire gauze.

As a result of this procedure the particles of the sediment adhere both to one another and to the surface of the filter paper just firmly enough to prevent any from falling into the water, but are sufficiently loosely held together to

allow the larvae to work their way out of the sediment. It is of great importance for the recovery of the maximum number of larvae to place this preparation into the Baermann apparatus as soon as the actual wetness has disappeared, as, should it be allowed to become even partially dry the particles of the sediment adhere together so closely that some of the larvae are unable to make their way out. This freeing of the living larvae is a gradual process, about half of them being ready to withdraw from the bottom of the funnel in 24 hr. time and almost all at the end of a week. The rest of the original sediment, however, remains above the screen, and the water in which the larvae are drawn off is perfectly clear and free from everything except the free-living nematodes, strongyloid larvae, rotifers and other living things that have actively made their way out of the sediment on the filter paper.

Microscopical examination

This examination is carried out under the dissecting microscope in small petri dishes having parallel lines scratched across the bottom. A magnification of 16 or 25 diameters is found to be sufficient, the parasitic larvae being picked out with a fine pipette as the lined petri dish is moved backwards and forwards under the objective, along the successive spaces between the parallel lines. Occasional larvae may require to be examined under a higher magnification for identification; but with increasing experience these occasions will be very few.

Where relatively few larvae are present the whole of the material is examined but where many are present, as, for instance, in the material from the bucket to which the thousand larvae were originally added, it may be found sufficient to examine only one tenth part of the whole amount.

The number of larvae per pound of the original herbage is then worked out by the following formula:

$$B \times \frac{1000}{A-B} \times \frac{16}{W} = \text{number of larvae per pound of herbage,}$$

where A represents the number of larvae recovered from the bucket to which one thousand had been added, B the number of larvae recovered from the bucket containing the other half of that sample, and W the weight of half of the original sample.

Discussion

Work in this field of investigation was begun during the spring of 1936 since when data have been collected in whatever time has been available for that purpose: the results, which it is hoped shortly to publish, give the numbers of larvae per pound of herbage that have been recovered from various pastures under different conditions of grazing.

Biometric tests will have to be applied before the reliability of the test for

the estimation of pasture infection is really known but a comparison of the results obtained from the two separately collected samples suggest it to be at least as good as many other biological tests that have proved their worth for investigational purposes, and the results already obtained may justly be regarded as informative.

Although the number of larvae per unit weight of herbage appears to be the most useful figure the number of larvae per unit area will, doubtless, also prove of value in helping towards a full understanding of the circumstances governing the rate of intake of larvae by the grazing animal. This second figure can be found by applying Stapledon's[1] technique for estimating the amount of herbage per unit area, and making a simple calculation on the estimated number of larvae per unit weight of herbage.

The technique which has here been described for the separation of larvae from the muddy sediment is rather slow, some eight or nine days being required for the whole process if the maximum number of larvae is to be recovered: a flotation method could be used instead of the filter paper method but is less efficient as fewer larvae are recovered, and the final liquid in which the larvae are obtained is so dirty that the difficulty of the microscopical examination is greatly increased. It is considered better, where a result is required more speedily, to use the filter paper method but to allow only one or two days in the Baermann apparatus instead of the usual seven; a certain proportion of the larvae will be left behind in the sediment but the control half sample to which 1000 larvae have been added will make the necessary adjustment, and the accuracy of the result will not be greatly affected.

This method of gauging the efficiency of the process by the addition of 1000 larvae to half of one sample should always be included not only because of what has just been mentioned but also as a control on the variable separation of the larvae from the herbage and from the sediment, the efficiency of this process being influenced to a considerable extent by the nature and amount of the material that is being handled.

For these same reasons it is important to divide both of the separately collected samples of herbage into two so that all of the larvae will have an equal chance of coming successfully through the process and being collected at the end. Hence, collector A's sample is divided into two, to one of which 1000 larvae are added, and collector B's sample is also divided into two although no larvae have been added, four Baermann funnels being used for each test.

[1] Although referred to in previous publications, Davies (1931, 1939) and Jones (1932), this method does not appear to have been fully described. It consists of choosing fine areas of about one-hundredth of an acre each, evenly spaced over the surface of the field which is to be tested, and cutting the herbage from three square yards in each of those areas. The three sample patches in each of the chosen areas are marked at random by means of a wooden frame enclosing one square yard, the frame being either thrown each time or placed on the ground with the eyes shut.

As the moisture content of herbage is very variable, considerable advantage is to be derived from working on a dry-matter basis; the grass is therefore dried before weighing and the weight of dry matter per acre calculated from the sample cut from the fifteen square yards.

The two lots of larvae from B's two funnels, however, may be mixed together before the microscopical examination is carried out.

The most obvious use to the practical agriculturalist of data derived from this test is in providing information on the relative extent of infestation of any given field. For instance, data collected up to the present time suggest that an average sheep pasture towards the end of the summer carries about 200 infective larvae per pound of herbage, a heavily infected one carries up to 500, and one where sheep suffering from acute parasitic gastritis are grazing may carry between 1000 and 2500 larvae per pound of herbage.

The significance of the data acquired up to date has already been discussed in two previous papers (Taylor, 1938 *a*, *b*) but the most surprising outcome of the investigation has been the information acquired on the high rate of intake of infective larvae by the grazing animal. The insight that it has given into the important bearing of the quantity of herbage in a field upon the rate of intake of larvae—a significant point which does not appear to have been previously recognized—and the extent of the beneficial effect of grazing infected pasture by unsuitable host animals has also been made clear. There is, obviously, much to be learned in other directions concerning the development of strongyloid disease in grazing animals from the further application of this technique and it is in the hope that the work will be taken up elsewhere and that other investigators may be able to improve the technique that the author's method is published here at the present time.

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THE EARLY STAGES OF *LIMNOPHORA EXURDA* PAND. (DIPTERA, ANTHOMYIDAE)

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(With 11 Figures in the Text)

Although the larvae and puparia of several species of *Limnophora* have been described by Johannsen (1935, *L. aequifrons*, *L. torreyae* and *L. discreta*) and Marchand (1923, *L. discreta*), a detailed study of the structure of the larval mouthparts has not been made and the habits of the larvae are almost unknown.

Larvae and puparia of *L. exurda* Pand. (Collin, 1921) were collected on the south coast of Co. Cork, Eire, and have provided material for some biological observations and for morphological study. The larvae were found amongst tufts of moss and liverworts growing in wet situations, especially in the dense tufts growing in or near small cascades of fresh water falling over rocks into the sea. These mossy tufts were constantly wet with fresh water and were generally so situated that they were exposed to sea-water spray. The larvae move with great agility between the stems of the moss, aided by spinous protuberances on the ventral surface, and they can anchor themselves firmly to leaves or branches by a pair of ventral, spinous processes at the posterior end of the body. The puparia are found attached to stems of moss by the posterior processes of the larvae.

Observations on living larvae showed that they are carnivorous in habit as they were seen to attack and consume other small larvae and small oligochaetes confined with them. The mode of attack and destruction of prey is similar to that usual among carnivorous anthomyid larvae (Keilin, 1917; Tate, 1935): the prey is seized by being encircled by the anterior segments of the *Limnophora* larva which then perforates the body wall with the sharp oral hooks and proceeds to suck and scrape out the body contents.

Unfortunately, eggs were not found, so it was not possible to determine the duration of larval life, or whether the usual larval trimorphism is absent in this species as it is known to be in some other carnivorous anthomyid larvae, namely, *Mydaea urbana* and *Myiospila meditabunda* (Portchinsky, 1910); *Melanochelia riparia* (Keilin, 1917); *Phaonia mirabilis* (Tate, 1935) and *Mydaea pagana*, *Myiospila meditabunda* and *Hebecnema umbratica* (Thomson, 1937). In all of these larvae either the first larval stage, or the first and second larval stages, are absent from the life history. Some very small

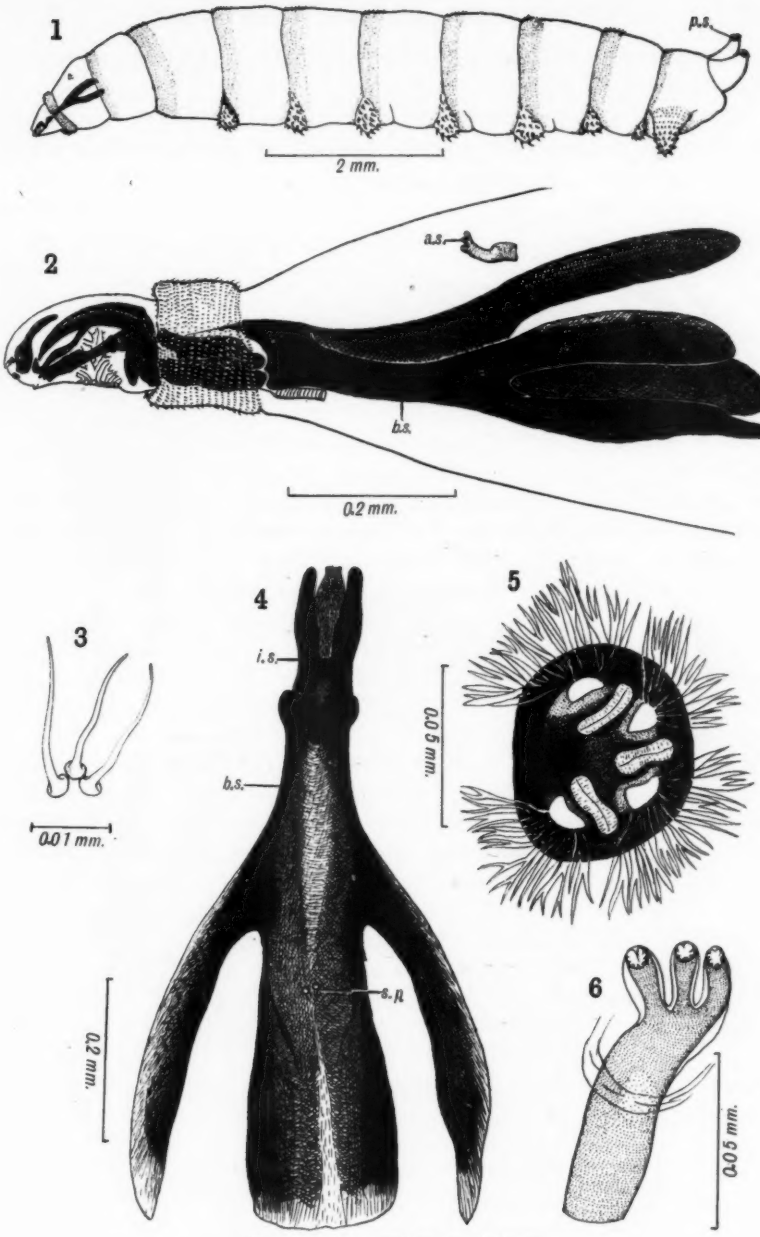
Limnophora larvae which were collected were found to be amphipneustic and to have the buccopharyngeal armature similar to that of the mature larvae, so it is probable that trimorphism is absent in this species also. The exact length of pupal life is not known, but imagines emerged from puparia about two weeks after they had been collected.

The mature larva is about 1 cm. long, is yellowish white in colour, and has a head, three thoracic and eight abdominal segments (Fig. 1). The anterior part of the prothoracic segment has a collar formed of many rows of backwardly directed spines (Fig. 2); and three to six rows of similar spines encircle the anterior margin of all the succeeding segments. On the ventral surface of each of the first seven abdominal segments there are paired retractile protuberances which bear strong backwardly directed hooks (Fig. 1). The eighth abdominal segment has a pair of ventro-lateral processes covered with recurved spines, which function as locomotory and prehensile organs; and there is a pair of posterior-dorsal, curved processes on which the postabdominal spiracles are borne terminally (Fig. 1, *p.s.*). The anus opens ventrally on the eighth abdominal segment between the ventral processes. The chitin of the body wall is thick and firm and shows conspicuous longitudinal striations.

The head is composed of two lobes separated by deep median dorsal and ventral grooves. The antennae are formed of a small basal segment with a brown chitinized wall which is surmounted by a thin-walled bell-shaped vesicle (Fig. 7, *A.*). The maxillary palps are formed of annular bands of chitin enclosing groups of sensory papillae (Fig. 7, *m.p.*). Ventral and posterior to the maxillary palps there is a pair of papillae representing the sensory organs "C" of Keilin (Fig. 7, *C.*). A pair of labial palps project from the posterior part of the ventral groove, beneath the oral opening, and terminate in sensory processes (Figs. 7, 8, *l.p.*). From the oral opening a series of oral grooves extend in a fan-like manner on each side.

Two groups of setae occur on the ventral surface of each thoracic segment. Each group consists of three short setae and they are connected with the imaginal disks of the legs and represent the sensory vestiges of the thoracic legs (Keilin, 1915, 1917).

The respiratory system is amphipneustic and there are a pair of prothoracic and a pair of postabdominal spiracles. Each prothoracic spiracle has three spiracular lobes and faint internal and external scars (Fig. 6). The postabdominal spiracles are situated at the ends of the curved, tapering, processes of the eighth abdominal segment (Fig. 1, *p.s.*). Each spiracle consists of a dark peritreme containing three radiating spiracular clefts (Fig. 5). Each cleft is covered by a thin membrane pierced by a fine medial longitudinal slit which is the actual respiratory opening. There is a definite external scar, and from four areas of weak chitin in the peritreme very numerous palmate hairs radiate. These hairs are very numerous and large in this larva, a fact which is probably to be correlated with the semiaquatic mode of life, as the

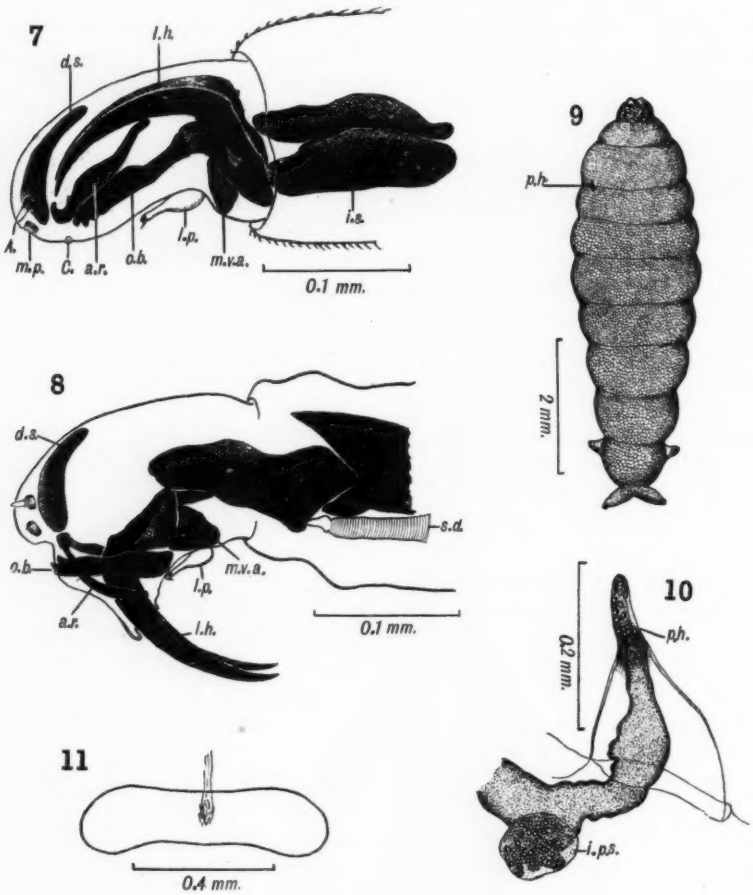


Figs. 1–6. *Limnophora exurda* larva.

Fig. 1. Lateral view of mature larva.
Fig. 2. Lateral view of head and buccopharyngeal armature.
Fig. 3. One of the groups of three setae which form the sensory vestiges of the thoracic legs.
Fig. 4. Ventral view of the basal and intermediate sclerites of the buccopharyngeal armature.
Fig. 5. Surface view of a postabdominal spiracle. Fig. 6. Anterior spiracle.

hairs are hydrofuge and hence provide a large area to support the postabdominal spiracles above the surface of the water.

The buccopharyngeal armature includes a long, strongly chitinized basal sclerite which is narrow dorso-ventrally and of which the lateral wings are



Figs. 7–11. *Limnophora exurda*, larva and puparium.

Fig. 7. Head of larva with oral sclerites retracted.
Fig. 8. Head of larva with oral sclerites extruded.
Fig. 9. Puparium, dorsal view.
Fig. 10. Respiratory horns and intrapupal spiracles from puparium.
Fig. 11. Anal plate of larva—from puparium.

deeply excavated posteriorly (Figs. 2, 4, *b.s.*). The anterior bridge of the basal sclerite is complete. The ventral wall of the pharynx is strongly chitinized and there are no longitudinal pharyngeal ridges (Fig. 4, *b.s.*). On each side

of the mid-ventral line, a little more than half-way from the anterior end, there is a sensory pit (Fig. 4, *s.p.*). The basal sclerite has deep rectangular excavations in each side of the anterior end with which the lateral bars of the very stout, heavily chitinized, H-shaped intermediate sclerite (Figs. 4, 7, *i.s.*) articulate. The common salivary duct opens at the cross-bar of the intermediate sclerite (Fig. 8, *s.d.*).

The lateral hooks are long, slender, densely chitinized and sharply pointed (Figs. 7, 8, *l.h.*). There are square sclerites attached to the anterior edges of the basal parts of the lateral hooks with which articulate a pair of stout oral bars, each terminating anteriorly in three recurved teeth (Figs. 7, 8, *o.b.*). A stout median ventral arc unites the bases of the lateral hooks (Figs. 7, 8, *m.v.a.*). Paired rods, forming an anterior ribbon, lie dorsal and partly anterior to the oral bars and extend from near the middle of the lateral hooks to beyond their tips (Figs. 7, 8, *a.r.*). The ventral part of the dorsal groove between the two lobes of the head is strongly chitinized and forms an accessory dorsal sclerite (Figs. 7, 8, *d.s.*). When the mouthparts are extruded the lateral hooks project ventro-posteriorly, the median ventral arc is pulled backwards, the oral bars project forwards and outwards so that the terminal teeth act as barbs to prevent the escape of the prey, and the anterior ribbon encircles the basal region of the blades of the lateral hooks.

The puparium is light brown, is not very heavily chitinized, and is about 8 mm. long by 2·5–3 mm. wide. The head and first two thoracic segments contract to form a dark knob at the anterior end and the third thoracic and the eight abdominal segments are well marked by annular constrictions (Fig. 9). The puparium is widest at the level of the second abdominal segment and then gradually narrows towards the posterior end. The last segment is very similar to that of the larva, and the dorsal spiracular processes and the ventral locomotory processes are retained and the latter serve to anchor the puparium to stems of moss. A pair of large dark respiratory horns, bearing numerous spiracular papillae, projects from near the anterior margin of the second abdominal segment; while, internally, intrapupal spiracles, bearing many spiracular papillae, are connected with the felt chambers (Fig. 10, *i.p.s.*). The surface of the puparium is ornamented with an irregularly hexagonal, raised network (Fig. 9). The adults emerge from the puparium by two splits at right angles to each other; a circular one passing around the middle of the first abdominal segment and a transverse horizontal split extending from the anterior end and meeting the circular split posteriorly.

DISCUSSION

Keilin (1914, 1915, 1917) has shown that a close correlation exists between the morphological characters and the mode of life of anthomyid larvae. Such a correlation is clearly discernible in *Limnophora exurda* larvae in which the observed carnivorous mode of life is reflected in the morphological characters. The thick, firm, longitudinally striated cuticle and the presence of paired

ventral, spinous, protuberances which help to secure the prey are features common to carnivorous forms. It is in the buccopharyngeal armature, however, that the most apparent adaptations are to be seen. The ventral surface of the basal sclerite is smooth and has no trace of the longitudinal pharyngeal ridges which are present in semi-carnivorous (Keilin & Tate, 1930) and saprophagous forms but do not occur in carnivorous larvae. The strongly chitinized, stout, intermediate sclerite and the structure and arrangement of the oral sclerites also indicate a carnivorous habit. The oral sclerites consist of long, slender, sharply pointed lateral hooks and accessory pieces comprising a pair of stout oral bars articulating with the lateral hooks through small square sclerites; paired sclerites forming an anterior ribbon; and a complete median ventral arc uniting the bases of the lateral hooks. The importance of the structure of the median ventral arc as a clue to the habits of anthomyid larvae has been emphasized by Thomson (1937), who points out that it is in the form of a complete bridge in carnivorous and in semi-carnivorous forms, whereas it is formed of two separate sclerites in purely saprophagous larvae. The small number of lobes in the anterior spiracles and the small size of the postabdominal spiracles are other characters of less importance which indicate a carnivorous mode of life (Thomson, 1937).

In mode of life and in morphology larvae of *L. exurda* very closely resemble those of *Melanochelia riparia* as described by Keilin (1917). The resemblance is so close that a detailed examination is necessary to differentiate the two forms. The most obvious difference is seen in the presence of the accessory dorsal sclerite, formed by the heavy chitinization of the dorsal head groove, in *Limnophora exurda* larvae which is absent in larvae of *Melanochelia riparia*. The puparia of the two flies are also remarkably alike, but differ in the puparium of *M. riparia* showing three thoracic segments, whereas in *Limnophora exurda* only one thoracic segment remains visible in the puparium.

Summary

The larvae and puparia of *Limnophora exurda* are to be found in tufts of wet moss or liverworts in or near small waterfalls.

The larvae are carnivorous and exhibit the characteristic morphological characters of carnivorous anthomyid larvae.

Acknowledgement. I wish to express my thanks to Mr J. E. Collin, Newmarket, for identifying the imagines.

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Key to the Lettering of Text-figures

A. antenna; *a.r.* anterior ribbon; *a.s.* anterior spiracle; *b.s.* basal sclerite; *C.* sensory organ "C"; *d.s.* dorsal sclerite; *i.s.* intermediate sclerite; *i.p.s.* intra-pupal spiracles; *l.h.* lateral hooks; *l.p.* labial palp; *m.p.* maxillary palp; *m.v.a.* median ventral arc; *o.b.* oral bar; *p.h.* prothoracic respiratory horns of nymph; *p.s.* posterior spiracles; *s.d.* salivary duct; *s.p.* sensory pit.

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ON SOME AMERICAN GENERA OF THE STREBLIDAE AND THEIR SPECIES, WITH THE DESCRIPTION OF A NEW SPECIES OF *TRICHOBIUS* (DIPTERA, ACALYPTERAE)

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(With 4 Figures in the Text)

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Introduction

In the present paper I discuss the identity and systematic position of *Synthesiostrebla amorphochili* Townsend, *Speiseria ambigua* Kessel and *Lemosia setosa* Pessôa & Galvão. Besides, I include in this paper a revision of the species of the genus *Paratrichobius*, which structurally is more or less closely related to the genus *Synthesiostrebla*.

The figures illustrating this paper were made with the aid of a camera lucida from specimens mounted in Canada balsam. The wings of these specimens were mounted in Euparol, separately from the body, but on the same slide.

For the assistance given to me in the preparation of this paper I express my thanks to Dr C. H. Townsend of Itaquaquecetuba, Sao Paulo, Brazil, and to Dr C. H. Curran of The American Museum of Natural History.

The identity and systematic position of *Synthesiostrebla amorphochili* Townsend and *Speiseria ambigua* Kessel

Synthesiostrebla amorphochili Townsend was described from a single specimen collected in Peru. As this streblid has never been recorded since the

original description was written, it is either very rare or has been misidentified and described under a different name. According to the characters given in the original description, it is very closely related to *Speiseria ambigua* Kessel, from which it differs by only one character—the presence of a pair of strong teeth in the middle of the anterior margin of the mesonotum, which fit into a corresponding depression on the head. An examination of the thorax of *Speiseria ambigua* showed that the anterior margin of its mesonotum is also produced in the middle and fits into the depression of the posterior part of the head when the latter is elevated. As the type specimen of Townsend was preserved dry, it occurred to me that the tooth-shaped processes described by him might have been produced by distortion of the thorax and that the form was really the same as that subsequently described by Kessel, from the spirit-preserved specimen, as *Speiseria ambigua*. In order to settle this matter, I wrote to Dr Townsend, and with his kind help located the type specimen of *Synthesiostrebla amorphochili* in the American Museum of Natural History. Then I wrote to Dr Curran, asking him to compare it with *Speiseria ambigua*. Dr Curran very kindly examined these two insects, and subsequently sent to me the following note: "I have been able to examine the type of *Synthesiostrebla amorphochili* and find that it is the same as *Speiseria ambigua*. Unfortunately the type is not in the best of condition but there can be no doubt that the two are the same." This proves without any doubt the identity of the forms described by Townsend and Kessel, and therefore, the name of *Speiseria ambigua* Kessel should be considered as a synonym of *Synthesiostrebla amorphochili* Townsend.

The genus *Synthesiostrebla* belongs to the subfamily Trichobiinae (Jobling, 1936), where, according to its character, it can be placed between the genus *Trichobius* Gervais and the genus *Paratrichobius* Costa Lima. Its head, wings and especially the fore and the middle legs resemble those of the genus *Trichobius*, from which it can be easily separated by the structure of the thorax and the greatly elongated hind legs. From the genus *Paratrichobius* it differs by the form of the thorax, which is broader than long, has very well-developed humeral calluses and complete median and the mesonotal sutures, and also by the presence of the long, thin setae on the outer side of the tibiae of the fore and the middle legs and the absence of a distinct diagonal row of very strong, darkly pigmented setae on the femora of the forelegs. The following re-definition of the genus *Synthesiostrebla* is based on the comparison of its structure with the other closely related genera.

Synthesiostrebla Townsend, 1913

Speiseria Kessel, 1925

Head more or less triangular in outline when examined from above; its dorsal surface subdivided into four distinct, sclerotized subregions and strongly produced in the postero-lateral parts; occiput depressed. Eyes faceted, not

projecting beyond the lateral margin of the head. Thorax slightly broader than long. Anterior margin of the prescutum produced in the middle and fitting into the corresponding depression of occiput when the head is elevated. Humeral calluses distinct and conical. Median suture of the prescutum connected with the mesonotal suture which is complete in the middle. Sternopleura (*st.*) together form a triangular plate, of which the narrow apical part has an incurved margin. Wings normal, with six longitudinal and three cross veins; fifth and sixth longitudinal veins parallel. Tibiae of the fore and the middle legs with long, very thin outer setae. Femora of the legs with a few strong setae. Hindlegs strongly elongated, twice as long as the forelegs. Abdomen of the female sacciform, that of the male conical.

Type of the genus: *Synthesiostrebla amorphochili* Townsend.

Synthesiostrebla amorphochili Townsend, 1913

Speiseria ambigua Kessel, 1925

Body 2·2 and 2·6 mm. long (on slide) in male and female respectively. Sclerotized subregions of the dorsal surface of the head with strong setae and a few small ones bordering the postero-lateral produced part. The ventral surface of the head with ten long setae in the posterior part, behind the rostrum membrane, laterally to these it bears very small setae. Palps foliaceous, almost rounded, with long terminal setae. Labium as in Fig. 1, B, its labella (*l.*) as long as the theca (*th.*). Prescutum bare in the middle of the anterior part, otherwise very setose; the setae of its antero-lateral parts stronger than those arising in its posterior part. Scutum with small setae in the anterior part and very strong setae in the posterior part, of which those arising from its lateral borders are as long as the scutellar setae. Scutellum rhomboidal, with four usual setae, of which the middle two arise closer to its posterior border than the other. Sternopleura and pleurotrochantines beset with small setae, which are about as long as the distance between them.

Wings 2·0 and 2·3 mm. long in male and female respectively. Legs presenting no distinctive character.

Dorsum of abdomen with eight very small setae arranged in pairs and with eight long setae in front of the apical cone. Second sternite more or less triangular, with rounded, convex apex; its posterior border, in the lateral parts bearing very much thicker setae than those arising from the other parts of its surface. The membranous ventral surface of the abdomen beset with small setae and also bearing a few thin, long setae. Sternite-like plate of the posterior part of the abdomen convex, with long setae near the margin. Hypopygium of male abdomen conical, as in Fig. 1, C. Anteriorly to the base of the hypopygium, the ventral surface of the male abdomen fringed with strong, long setae.

The type specimen was collected from *Amorphochilus shnablii* Peters, in Piura, Peru. The specimens described by Kessel, as *Speiseria ambigua*, was

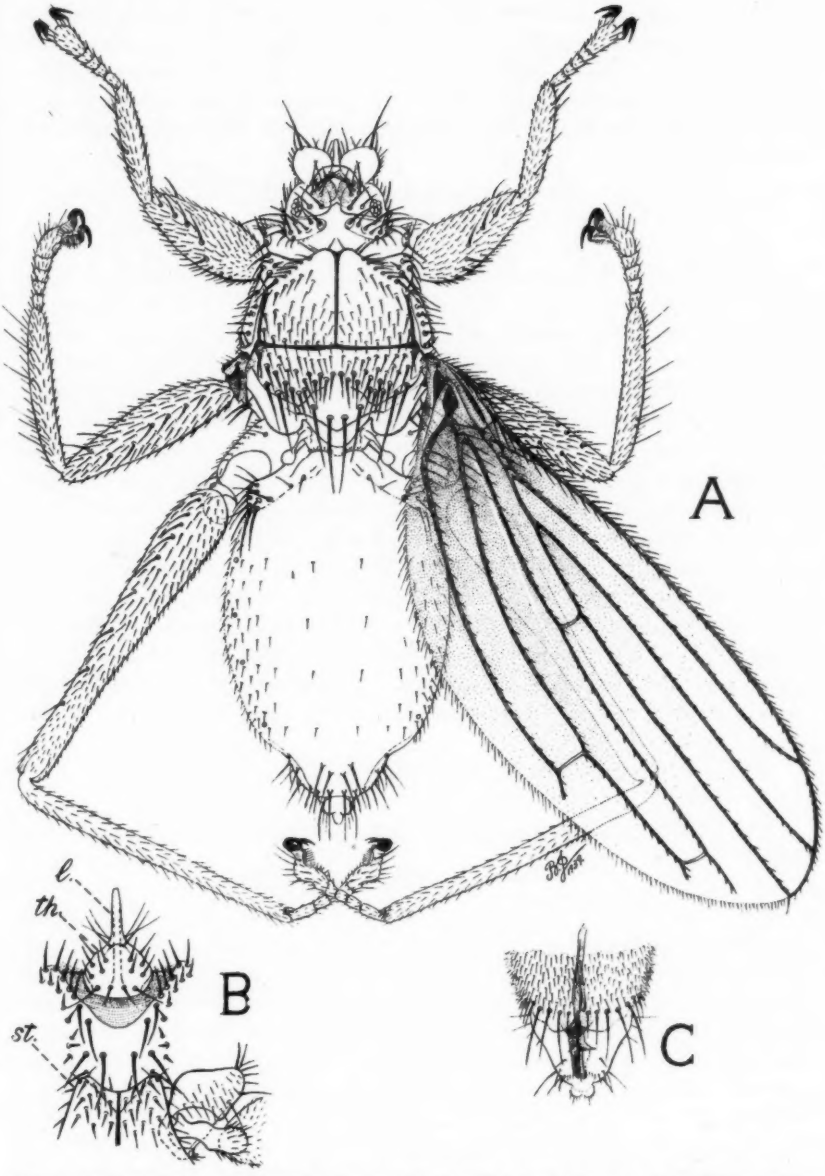

Fig. 1. *Synthesiostrebla amorphochili* Townsend. A. Dorsal view of female, ×40. B. Ventral view of labella (*l.*) and theca (*th.*) of labium, (*st.*) anterior part of sternopleura, ×66. C. Ventral view of posterior end of abdomen of male and its hypopygium, ×40.

from Pernambuco. The other records of this species are as follows: from *Carollia perspicillata* L., Porto Bello, Panama, recorded by Kessel; from the same host, Panama, collected by Major L. H. Dunn; from *Tonatia bideus* Spix, Kartabo, British Guiana, recorded by Curran, 1934; from *Glossophaga soricina* Pallas and *Hemiderma perspicillatum* L. (*Hemiderma perspicillatum* L.= *Carollia perspicillata* L.), S. Paulo, Brazil, recorded by Pessôa and Guimarães, 1936.

Paratrichobius Costa Lima, 1921

Trichobius Ribeiro, 1907

Head slightly oblong and distinctly broader in its posterior part when examined from above; the subregions of the dorsal surface widely separated, more than in *Synthesiostrebla*, with strong setae; the postero-lateral parts of the dorsal surface very strongly produced, more than in *Synthesiostrebla*; occipital part depressed. The ventral surface of the head with strong spine-like setae. Eyes faceted and projecting beyond the lateral margins of the head. Thorax as long as or slightly longer than broad, more or less ovoid when examined from above or below. Anterior margin of the prescutum distinctly or indistinctly produced in the middle. Median suture of the prescutum not reaching the mesonotal suture which is incomplete in the middle. The anterior projecting part of the sternopleura broad, with rounded or nearly transverse anterior margin. Wings normal, with six longitudinal and three cross veins; fifth and sixth longitudinal veins divergent towards the third cross vein. Tibiae of the fore and the middle legs without long, thin, outer setae. Femora of the forelegs with a distinct diagonal row of very strong, spine-like setae. Hindlegs twice or three times as long as the forelegs. Abdomen of both sexes sacciform.

Type of the genus: *Trichobius longicrus* Ribeiro.

Paratrichobius longicrus (Ribeiro, 1907) Costa Lima, 1921

Trichobius longicrus Ribeiro, 1907

Body 2·1 and 2·5 mm. long (on slide) in male and female respectively. Sclerotized subregions of the dorsal surface of the head with very strong, spine-like setae. The ventral surface of the head with a row of spine-like setae on each side of the rostrum membrane; the most posterior seta of each row twice as long as the other setae. The arrangement of the other setae as in Fig. 2, A. Palps rounded. Theca of labium cordiform, with strong setae in the anterior part and smaller setae in the middle; labella shorter than the theca (Fig. 2, A).

Prescutum with three strong setae in each antero-lateral corner and with a row of a few short, thick setae on each side of the median suture; its posterior part bearing minute setae behind the median suture and very much stronger setae laterally to these; its anterior margin distinctly produced in the middle.

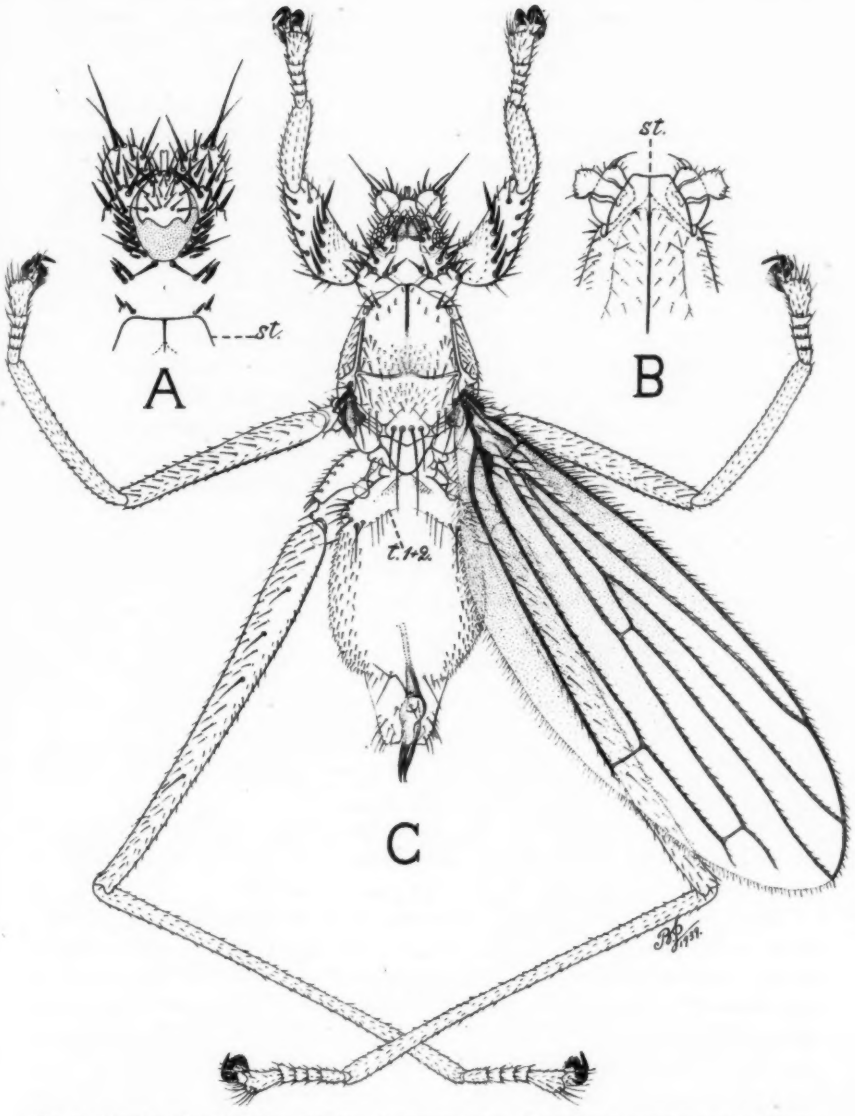

Fig. 2. *Paratrichobius longicrus* Ribeiro. A. Ventral view of head and anterior part of sternopleura (*st.*), ×66. B. Ventral view of anterior part of thorax, (*st.*) sternopleura, ×40. C. Dorsal view of male, (*t.* 1+2) tergite 1+2, ×40.

Scutum with small setae in the middle and very much stronger setae in its lateral parts. Scutellum small, with usual four setae arising from the middle. Pleurotrochantines and the middle part of sternopleura sparsely covered with thin setae. The anterior margin of the projecting anterior part of the sternopleura nearly straight (Fig. 2, B, *st.*). Femora of the forelegs with a row of tiny setae ventrally and parallel to the diagonal row of strong spine-like setae. Middle legs thin, nearly twice as long as the forelegs. Hindlegs very strongly elongated, a little more than three times as long as the forelegs.

Wings 2·4 and 2·6 mm. long in male and female respectively.

Ventral and lateral membranous parts of the abdomen beset with very small setae. The posterior border of the tergite 1 + 2 interrupted in the middle, with a few thin setae; its lateral rounded parts with strong setae. Apical cone of the abdomen with four long, dorsal setae. The sclerotized plates of the postero-ventral part of the abdomen small, rounded, with short and a few long setae. Abdomen of the male resembles that of the female, but bearing smaller setae, and ends in a large conical hypopygium (Fig. 2, C).

Type specimen was collected from *Artibeus jamaicensis jamaicensis* Leach, Brazil. The other records are as follows: from unknown species of bat, Micondla, Mexico; from *Vampyrops lineatus* Geoffroy, Portrevito, Villa Rica, Paraguay; from unknown species of bat, Joinville, Humboldt, Santa Catharina, Brazil; from *Artibeus perspicillatus* L. (*A. perspicillatus* L. = *Carollia perspicillata* L.), Ipiranga, S. Paulo, and from unknown species of bat, in S. Paulo Capital, Brazil, recorded by Pessôa & Guimarães (1936).

Paratrichobius dunni Curran, 1935

Speiseria dunni Curran, 1935

This species was referred by Curran to *Speiseria* which is now a synonym of *Synthesiostrebla*. My examination of the two paratypes showed that it belongs to the genus *Paratrichobius* Costa Lima.

This species differs from *P. longicrus* by its smaller size, different form of the anterior margin of the prescutum and more distinctly by the structure of the hindlegs, which are only twice as long as the forelegs.

Body 1·7 and 2·0 mm. long (on slide) in male and female respectively. Head as in *P. longicrus*, with the exception of the chaetotaxy of the ventral surface, which is as in Fig. 3, B. Palps narrowly pointed, with long terminal seta. Theca of labium bears uniform setae on the ventral surface and four very thin, long setae in the anterior part near the labella. Anterior margin of the prescutum slightly produced in the middle. Surface of the prescutum with uniform setae in the anterior part and with many much smaller setae in the posterior part behind the median suture. Scutum with small setae in the middle and a few strong setae near the lateral margins. Scutellum more rhomboidal than that of *P. longicrus*.

The projecting anterior part of the sternopleura broadly rounded (Fig. 3,

B, *st.*). Forelegs with three or four very small, thick setae at the base of the diagonal row of strong spine-like setae. Femora of the middle legs slightly thickened in the middle. Hindlegs twice as long as the forelegs.

Wings 1·5 and 1·7 mm. long in male and female respectively.

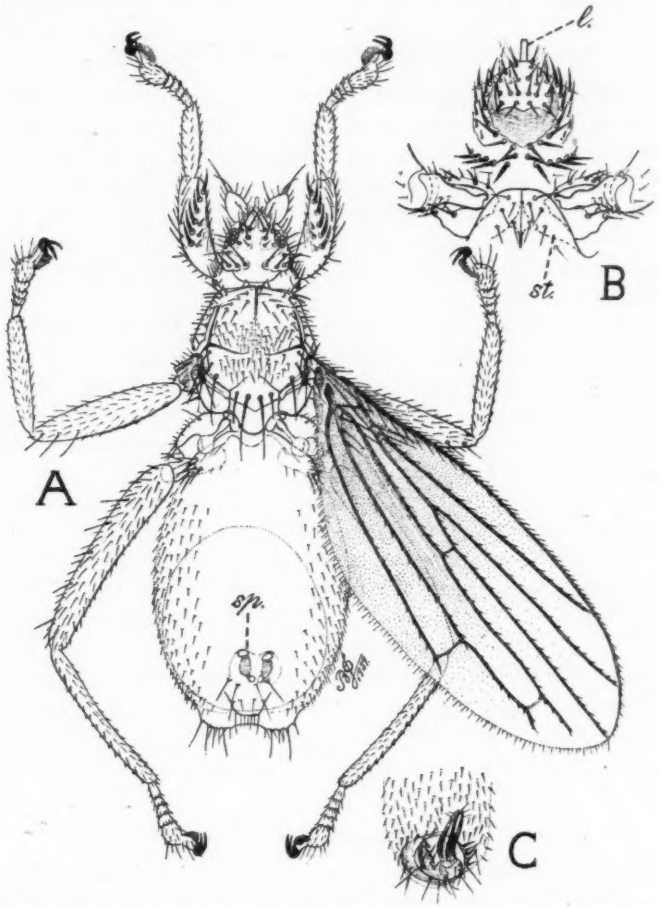

Fig. 3. *Paratrichobius dunni* Curran. A. Dorsal view of female, dotted line indicates position of larva in abdomen, (*sp.*) spiracles of larva, ×40. B. Ventral view of head and anterior part of thorax, (*l.*) labella, (*st.*) sternopleura, ×66. C. Posterior end of abdomen of male, ×40.

Abdomen of the female has the same structure as that of *P. longicrus*, but with weaker setae. Abdomen of the male cylindrical, with ventrally attached hypopygium (Fig. 3, C).

The holotype and two paratypes, from either *Pteropteryx canina* Wied. or *Uroderma bilobatum* Peters, El Real, Panama, collected by H. C. Clark.

The other paratypes, from *U. bilobatum* Peters, Summit, Canal Zone; and from *U. bilobatum* Peters and *Artibeus jamaicensis jamaicensis* Leach, Panama, collected by Major L. H. Dunn. All these specimens are preserved in the American Museum of Natural History, with the exception of two, which are in my collection.

On **Lemosia setosa** Pessôa & Galvão, 1936

According to the original description, this species resembles *Metelasmus pseudopterus* Coquillett (1907), from which it differs by only one character—the presence of the antennae. In the identification of their specimen the authors of this species were misled by the incomplete description of *M. pseudopterus* by Coquillett, and by the re-description of the same species by Séguy (1927), who overlooked the presence of the antennae in their specimens. In my paper (1936) I described the antennae of *M. pseudopterus* and also indicated their structure and position in the drawing of the head.

After comparing the description and the drawing of *Lemosia setosa* with those of *Metelasmus pseudopterus* given by Coquillett, Séguy and by me, it became evident that the form described by Pessôa & Galvão was identical with those studied by the authors just mentioned. Therefore the name *Lemosia setosa* Pessôa & Galvão should be regarded as a synonym of *Metelasmus pseudopterus* Coquillett.

In order to avoid further confusion of *M. pseudopterus*, it is necessary to mention here that Coquillett, Séguy, and Pessôa & Galvão overlooked the eyes in their specimens. These organs were described in my paper as single-faceted; they are indistinct in the unmounted specimen.

With the inclusion of *Lemosia setosa* in the synonymy of *Metelasmus pseudopterus*, we have now the following records of the latter species: Type specimen from *Artibeus lituratus* Lichtenstein, Paraguay; from unknown species of bat, Martinique (Séguy); from *A. perspicillatus* L. (*A. perspicillatus* L. = *Carollia perspicillata* L.) Mogy das Cruzas, S. Paulo, Brazil (Pessôa & Galvão); from *Artibeus jamaicensis jamaicensis* Leach, Puente Natural, Panama (Jobling).

Trichobius sphaeronotus sp.n.

Structurally this new species resembles *T. sparsus* Kessel (1925), which was revised by me (1938) together with the other species of the genus. It differs from the last-mentioned species by the following characters: its thorax is more globular; the scutum bears a single **W**-shaped row of very minute setae, which passes in front of the scutellum and extends to the antero-lateral corners of the scutum; finally, by the position of the third cross vein, which does not form an angle of 55 degrees with the fifth longitudinal vein as in *T. sparsus*.

Body 1·9 and 2·5 mm. long (on slide) in male and female respectively. Dorsal surface of the head not subdivided into the sclerotized subregions,

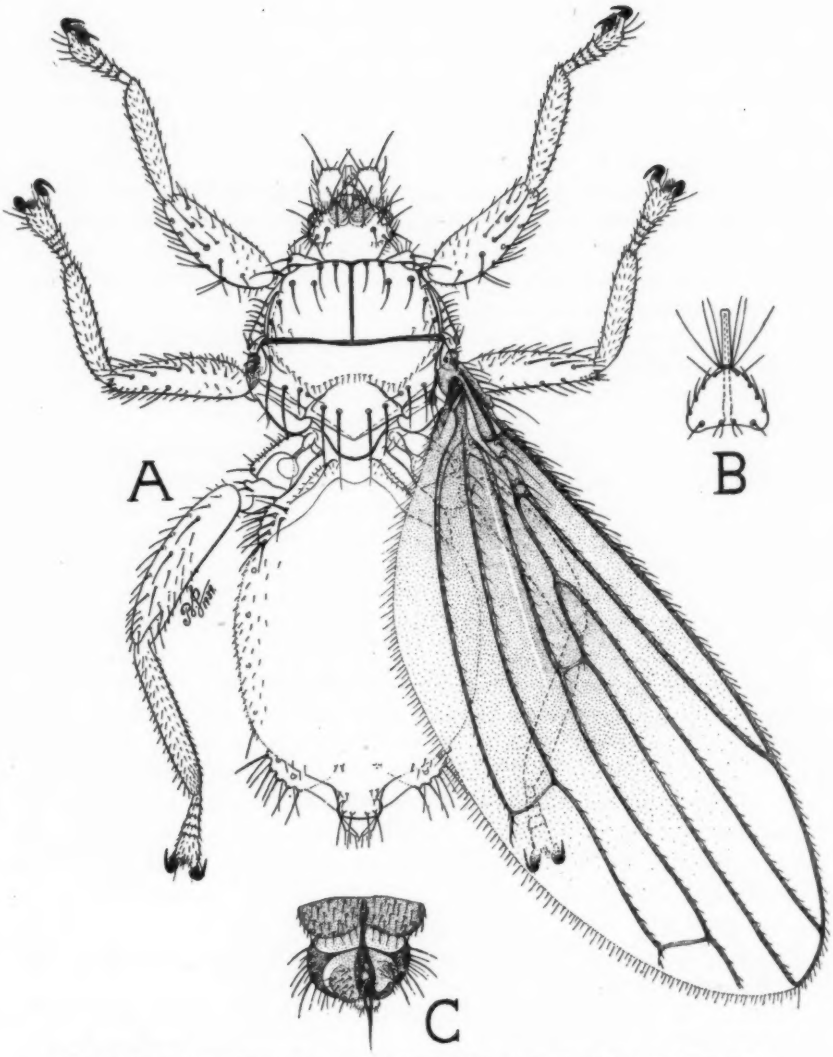

Fig. 4. *Trichobius sphaeronotus* sp.n. A. Dorsal view of female, ×40. B. Labium, ×66. C. Ventral view of posterior end of abdomen of male, ×40.

slightly elevated behind the antennae and produced in each postero-lateral part, with rather strong setae; a few small setae bordering the produced parts. Eyes large-faceted, projecting beyond the lateral margin of the head. Theca of labium cordiform, labella about as long as the theca (Fig. 4, B).

Thorax looks spherical when examined from above. Median suture of the prescutum varies; in some specimens it is distinctly, in others indistinctly, connected with the mesonotal suture. Each half of the prescutum bears eight very strong setae, of which four arise from the anterior margin, two behind these and two near the lateral margin; besides, there are two very small setae in each postero-lateral corner. Scutum with a single **W**-shaped row of very minute setae and a few very strong setae in the postero-lateral parts. Scutellum rhomboidal, with usual four long setae arising from its middle part. Sternopleura and pleurotrochantines with small, thin setae. Legs normal, the dorsal surface of femora with strong setae.

Wings 2·4 and 2·7 mm. long in male and female respectively; third cross-vein slightly inclined towards the base of the wing, but not forming an angle of 55 degrees with the fifth longitudinal vein; fifth and sixth longitudinal veins slightly divergent towards the third cross-vein.

Abdomen of the female sacciform, the setae of its venter as long as the distance between them. The sclerotized plates of the posterior part of the abdomen very distinct, with very strong setae in their dorsal half. Apical cone of the abdomen as in drawing 4, A. Abdomen of the male nearly cylindrical, with slightly stronger setae on its venter than those arising from the same part of the abdomen of the female; it ends in a hemispherical hypopygium, in front of which the ventral surface has a sternite-like setose plate (Fig. 4, C).

Seven specimens were examined. They were collected by Mr H. Hoogstraal, from *Leptonycteris nivalis* de Saussure, in Cerro Potosi, 9000 alt., Nuevo Leon, Mexico. Two specimens, a female and a male were designated as the holotype and the allotype respectively, and they will be deposited in the collection of the National Museum in Washington. All the other specimens were designated as the paratypes, of which three are in the collection of the University of Illinois and two in my collection. For presenting these last specimens to me I take this opportunity to express my thanks to Mr H. Hoogstraal of the University of Illinois.

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TURNING SICKNESS OF CATTLE AND *TRYPANOSOMA THEILERI*

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The disease known as Turning Sickness was first recorded by Mettam (1934) in this journal and later more fully described by Mettam & Carmichael (1936).

The condition has been defined as a protozoan encephalitis of cattle and one of the most striking features of the disease is the demonstration of schizonts indistinguishable from those of East Coast fever in the cerebral lesions of affected animals.

Since the 1936 publication mentioned above numerous cases have been investigated at this laboratory and many of these, but not all, have shown the typical schizonts or Koch's bodies in the brain, whilst the histopathology has been typical in all cases. An exception to this series forms the subject of this paper in so far that the symptoms were characteristic of turning sickness but the brain lesions on post-mortem yielded large numbers of *Trypanosoma theileri* and no Koch's bodies.

The animal was a zebu cow about 6 years old and for 2 days showed typical turning movements in a clockwise direction with a radius of approximately 6 ft. The animal collapsed into coma and was destroyed.

Post-mortem examination revealed rather an emaciated bovine. There was marked gastritis and the stomach contained numerous strongyloid worms. The spleen was small and fibrous and weighed 255 g. only. The lymphatic glands were all slightly hypertrophied and on section oedematous. There were old infarcts in the renal cortex. The animal was pregnant about 7 months. The rest of the body with the exception of the brain disclosed nothing of importance. Smears taken from the blood, liver, spleen, lungs, heart, muscle, and glands were all negative.

Brain

The meningeal vessels were congested. On examination the lesion was found to consist of a roughly circular patch of haemorrhagic softening about the size of a walnut with a tendency to necrosis.

The lesion involved the head of the caudate nucleus and extended into the corpus striatum and laterally into the internal capsule as far as the lentiform nucleus.

Smears prepared from the affected area and stained with Giemsa revealed numerous trypanosomes (*T. theileri*) together with masses of crithidial and

leishmanoid forms. Some of the trypanosomes appeared to be degenerating, but the presence of the immature forms indicate active development in the brain substance.

HISTOPATHOLOGY

Sections through the lesion showed rupture of capillaries of recent occurrence with red blood cells scattered throughout the nervous tissue in the region of the haemorrhage. Following the haemorrhage there has been an infiltration of cells of the monocytic series which are phagocytosing debris of destroyed neuroglia cells and free erythrocytes. The neuroglia cells in the vicinity show karyokinesis and scattered throughout are a few polymorphs. Parts of the lesion show early signs of organization or gliosis but mainly there is a structureless area of necrosis. Outside the area of immediate softening there are intact vessels engorged with blood, some showing thrombosis and all showing a perivascular infiltration of monocytes.

Sections stained by Giemsa's method show masses of trypanosomes in various stages of development from the leishmanoid and crithidial forms to the mature parasite, mixed with monocytes, erythrocytes and a few polymorphs. Further removed from this area are seen numerous trypanosomes lying in the meshwork of glial fibrils.

Sections of the cerebral cortex well away from the lesion show marked congestion of the capillaries with varying degrees of perivascular infiltration, but no rupture of vessels can be observed and there are no trypanosomes in the surrounding brain tissue.

DISCUSSION

It is evident that the symptoms of turning sickness in cattle can be associated both with the schizonts of *Theileria* and also *Trypanosoma theileri*. Under normal circumstances this trypanosome can be considered non-pathogenic to cattle, but occasionally in the manufacture of rinderpest serum in animals having a lowered resistance they may produce definite symptoms of disease such as anaemia and wasting, and in these cases enormous numbers of parasites are seen in the peripheral blood (Carmichael, 1926).

Hoare (1936) points out that our knowledge about the multiplication of *T. theileri* is incomplete and quotes Carpano (1932). He states: "it would appear that the reproduction of the cattle trypanosome is similar to that of *T. cruzi*, namely it multiplies in the 'fixed' tissues (brain and lymph glands) as a leishmanial form by binary fission, later assuming the crithidial form, which in its turn gives rise to the typical trypanosomes in the blood".

A perusal of Carpano's (1932) paper reveals that he found *T. theileri* in various stages of development in the hypertrophied prescapular lymphatic gland of a presumably healthy Egyptian cow at a post-mortem at the Cairo abattoir. He further records in some detail the case of an Abyssinian cow which he examined 28 years previously. This animal showed symptoms of

a lethargic encephalitis and at post-mortem examination the brain showed an area of haemorrhagic softening in which the developmental stages of *T. theileri* were demonstrated. He describes leishmanial, plasmodial, leptomonad, crithidial and mature forms of the parasite. Apparently no sections were taken but the case appears to be a very similar one to that seen in Uganda.

The disease known as turning sickness is responsible for a not inconsiderable annual loss in Uganda and also in Kenya. So far all attempts to transmit the disease have failed and one is forced to consider whether species of *Theileria* or *T. theileri* are the primary cause of the condition or whether these protozoa are merely secondary invaders in a brain already infected by an agent such as a virus, the nature of which is at present obscure.

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THE MORPHOLOGY AND SYSTEMATIC POSITION OF *DOBELLINA MESNILI* NOV.GEN. (*ENTAMOEBA MESNILI* KEILIN, 1917)

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From the Molteno Institute, University of Cambridge

(With Plates XIII and XIV, containing Figs. 1–46 and Fig. I in the Text)

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I. Introduction

In 1917 Keilin described and figured a parasitic amoeba discovered by him in larvae of *Trichocera hiemalis* Meig. (the common "winter gnat") collected from a garden in Paris. Later he found the amoeba in larvae of *T. hiemalis* Meig. and *T. annulata* Meig. from several sources in Cambridge. He named it *Entamoeba mesnili*. He pointed out that, whereas it resembled the known entamoebae in its parasitic mode of life, in its well-developed lobopodia, and in the absence of a contractile vacuole, it differed from them in that it is multinucleate during the vegetative phase of its life cycle, and in the adhesive nature of the protoplasm at the posterior end of the body.

Prof. Keilin suggested to us that this interesting amoeba should be studied in greater detail and its systematic position revised in the light of our present knowledge of the Entamoebae. Some earlier attempts to obtain larvae of *Trichocera* parasitized by *Entamoeba mesnili* failed, but during the past year we have been fortunate in obtaining a wealth of material upon which the greater part of this study has been based. Prof. Keilin has generously placed at our disposal the preparations on which his description was founded, and also preparations from material which he obtained after the publication of his paper. Throughout this study he has been generous in help and encouragement.

As will appear from the following account, this parasite should no longer be placed in the genus *Entamoeba*. We propose, therefore, to erect for it a new genus and to name it *Dobellina* in honour of Mr Clifford Dobell, F.R.S.

II. Material

The larval stages of species of *Trichocera* (winter gnats) occur during the colder months of the year in moist situations rich in decaying organic matter, such as amongst decaying leaves and, especially, in rotting root vegetables. The best sources of material for the present work were found to be decaying roots of mangold-wurzels (*Beta vulgaris* var. *cicla*), either discarded from storage pits or left in the fields after harvesting, and decaying turnips and potatoes. Many larvae from different areas and different material were collected and examined for infection with *Dobellina mesnili*. It was found that there is a seasonal variation in the prevalence of the parasite and also that the distribution of the parasite may remain very localized. In fact larvae from one source may yield a large proportion of parasitized individuals whilst larvae from another source, only a short distance away, may be consistently free of parasites.

The greater part of the material utilized for the present work was collected from two main sources, A and B. Source A consisted of turnips which had been left in the ground until rotten and were subsequently dug up and left in a decaying heap together with other garden rubbish. Larvae were collected from this material during October and December 1938, but of sixty-seven larvae dissected none was found to be infected with *Dobellina mesnili*. More larvae were collected on 8 January 1939 and 33% of them were found to be infected (thirteen positive out of thirty-nine dissected). This material continued to yield infected larvae during January and February and in the latter month the infection rate was very high (eighteen infected out of twenty-five dissected, or 72%). It is interesting that larvae obtained from decaying potatoes situated within 10–15 yards of source A were examined throughout January but were never found to be infected with *D. mesnili* (forty-two examined).

Source B consisted of decaying mangold-wurzels. The first lot of larvae was collected from this material on 15 January 1939 but of the eighteen dissected none was infected with *D. mesnili*. Larvae were next collected on 29 January and of the forty-four dissected thirty-two (=73%) were infected with *D. mesnili*. This material yielded an excellent supply of infected larvae throughout February, different batches of larvae showing infection rates of 92, 85, and 83%. Further collections were made in April and May and infection rates of 20–38% were found. However, larvae of *Trichocera* became rare after May and of the few which were collected and examined none was infected with *Dobellina mesnili*. In all, 334 larvae were dissected from source B and of them 233 were infected, which gives an average infection rate of 70% over the whole period of collection. Larvae were also obtained from an old storage pit a short distance from source B but of the twenty dissected only three were parasitized by *D. mesnili*.

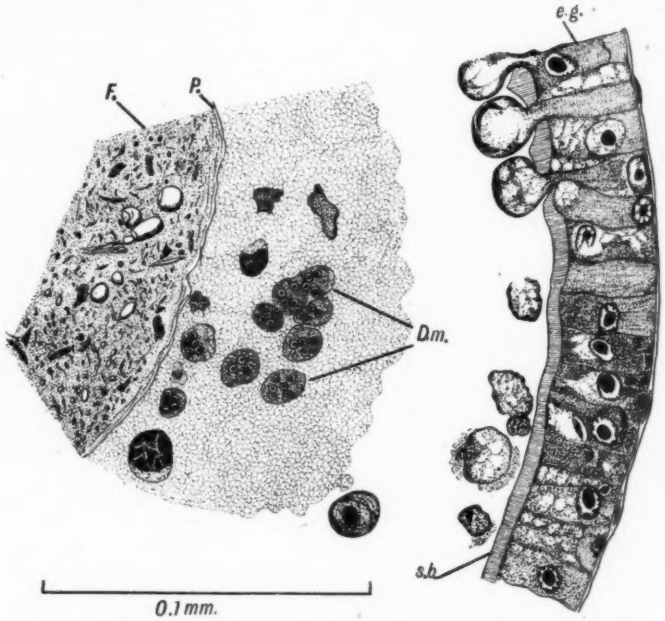
Occasionally infected larvae were obtained from other sources including

decaying leaves, rotting celery roots and rotting garden rubbish, but in no case were larvae found to be infected earlier in the winter than January or later in the year than May.

Imagines were reared from several batches of larvae collected from source B and were identified by Dr F. W. Edwards as *Trichocera regelationis* L.

III. METHODS

The amoebae live in the lumen of the gut of the *Trichocera* larvae. The great majority of them occur in the annular space between the peritrophic membrane and the epithelium of the gut (Text-fig. I), but it can be seen from



Text-fig. I. A portion of a transverse section through the gut of a *Trichocera* larva infected with *Dobellina mesnili* showing the localization of the parasites between the peritrophic membrane and the epithelium of the gut. *D.m.* group of *Dobellina mesnili* lying in coagulated exudate between the peritrophic membrane and the epithelium of the gut; *e.g.* epithelial cells of gut; *F.* food particles and detritus filling the peritrophic membrane; *P.* peritrophic membrane; *s.b.* striated border of epithelial cells.

sections of the gut that some amoebae may also be present within the peritrophic membrane where they lie amongst the detritus which forms the larval food. If a young, living, infected larva of *Trichocera* is compressed in a little saline solution between a slide and cover-slip and examined under the low power of the microscope, the amoebae can be seen moving actively in the space between the peritrophic membrane and the gut wall and being passively

driven to and fro by the peristaltic contractions of the gut. Often the amoebae are so numerous that they form dense masses completely filling the annular space. No parasites other than *Dobellina mesnili* are known to occur in this space so that *D. mesnili* may be considered to be present there in "pure culture".

To obtain material for smears the posterior segment of the body and the head of the larva were cut off and the gut drawn out and teased up in either the perivisceral fluid alone, or with the addition of a little serum saline (inactivated horse serum in 1:10 in 0·5% NaCl). Fixation in Schaudinn's solution with 5% glacial acetic acid for 10–20 min. gave the best results, both for smears and for whole guts for sectioning. Smears were stained in iron haematoxylin alone, or counter-stained with eosin or light green. Feulgen's reaction, according to the method described by Robertson (1927), was also used. Sections were stained with Delafield's haematoxylin.

IV. Morphology and life cycle of *Dobellina mesnili*

In hanging-drop preparations made in serum saline (see above) the amoebae remain alive and active for at least 24 hr. Our observations upon the living organism confirm Keilin's description. For a short period after their liberation from the teased-out gut of the host the amoebae remain rounded up and motionless, but usually within a few minutes streaming movements are visible in the endoplasm and a broad, hyaline, pseudopodium is formed. In most amoebae only one pseudopodium, directed anteriorly, is formed and movement is smooth and comparatively rapid. The pseudopodium is always formed of clear ectoplasm and is sharply defined from the endoplasm. In the majority of amoebae the endoplasm is closely packed with small refringent granules which are not visible when the organism is fixed and stained. The granules are carried along in the streaming movements of the endoplasm.

The endoplasm can be studied best in those individuals which are free from refringent granules, and in them it usually appears to be quite homogeneous but sometimes it appears to be slightly vacuolated. In individuals which have been fixed and stained (Figs. 3–5) these vacuoles are frequently visible. Food vacuoles have never been seen. *D. mesnili* appears to nourish itself entirely by osmosis. Inclusions of a chromatoid nature, such as are sometimes found in the precystic stage of *Entamoeba histolytica* (Dobell, 1919), and *E. aulastomi* (Bishop, 1932), and have been described by Geiman & Ratcliffe (1936) in some trophozoites of *E. invadens*, are never present.

In many individuals the posterior tip of the body appears to be adhesive, and groups of bacteria can be seen sticking to its surface (Figs. 3, 4, 6, 8).

In the majority of living *Dobellina mesnili* the nuclei are obscured by the granules in the endoplasm, but in individuals in which granules are absent or few the nuclei can be seen as spheres of greater density than the surrounding cytoplasm. In preparations stained with iron haematoxylin the nucleus

consists of a central, spherical, siderophilic karyosome separated from the delicate nuclear membrane by a clear, colourless halo. In the majority of individuals the nuclear membrane is difficult to detect, but in some forms (Fig. 12) it stains deeply. In the nuclei of some individuals (Figs. 5, 13 and 26) fine strands appear to radiate from the karyosome to the nuclear membrane. The application of Feulgen's nucleal reaction for nucleo-protein results in only an irregular layer on the surface of the karyosome being coloured red (Fig. 45). The karyosome, therefore, is not homogeneous, as preparations stained with iron haematoxylin suggest.

Dobellina mesnili may be uninucleate (Figs. 1–3) or, more frequently, multinucleate (Figs. 6, 9, 10–13). In rare cases there may be as many as 30 nuclei but individuals with 18–21 nuclei are not infrequent. Uninucleate amoebae are small, some being only 3·6μ in diameter, whereas multinucleate forms may measure 20–25 × 10–15μ. The average diameter of the karyosome is 1·2–1·5μ, and the total diameter of the nucleus may be 2·5–3μ, though it is not rare to find individuals (Figs. 6, 9) in which all the nuclei are very small. This may be the result of recent nuclear division. A few individuals (Figs. 7, 8) have been found in which the chromatin of the nucleus is loosely packed, producing a nucleus of greater than average size. These nuclei have a morula-like appearance. Their significance in the life history of the amoeba is not known.

The nuclei divide by the formation of delicate spindles. A pair of centrosomes appears and between them lies a very fine centrodesmose (Figs. 31, 32). The siderophilic substance of the nucleus becomes much reduced in quantity during division and the equatorial plate is small. It appears to consist of fine granules closely aggregated and there is no sign of individual chromosomes. The whole of the equatorial plate is stained red by Feulgen's nucleo-protein reaction, but the centrosomes and centrodesmose do not react (Fig. 46). From this it can be deduced that though the centrosomes are siderophilic they are achromatic, and that at this stage all the nucleo-protein is aggregated at the equator. Later the delicate spindles begin to elongate and the equatorial plate divides to form two daughter plates which become separated as the spindle elongates (Figs. 33, 34). Finally the centrosomes and the spindle disappear. After the disappearance of the spindles the chromatin of the daughter nuclei condenses and assumes at first a clover-leaf shape (Fig. 35) and later becomes spherical.

In the majority of individuals the nuclei divide simultaneously although in the final stages of division and during the reconstruction of the daughter nuclei individual nuclei may lag behind their fellows. Some amoebae have been seen in which only a proportion of the nuclei show signs of division whilst the remainder are in the resting condition, but this is rare. There is no indication at any stage of the life cycle of *D. mesnili* of any differentiation in function of the nuclei.

Keilin was of the opinion that the multinucleate amoebae are not precystic

stages, but that they are capable of undergoing division of the body. In support of this he gave figures (1917, Figs. 17–20) of 4, 6 and 8 nucleate amoebae which were dividing to form two daughter amoebae each containing half the original number of nuclei. We have confirmed his observations, and, in addition, we have found that the products of binary fission of the body may be equal (Figs. 14, 16, 21, 23, 25) or unequal (Figs. 15, 20, 24) in size; and also that the number of nuclei present in the two daughter amoebae may be equal (Figs. 14, 16, 21) or unequal (Figs. 15, 17, 18, 19, 20, 23, 24, 25). In some individuals (Figs. 15, 20) the division is so unequal, both with regard to the number of nuclei and the amount of cytoplasm, that the condition might be described as "budding". It is not infrequent to find a small, uninucleate or binucleate daughter amoeba being formed from a large, multinucleate amoeba. That Keilin suspected such a type of unequal division is indicated in his paper.

In addition to binary division we have also seen many examples of division of amoebae into three or four daughter amoebae in which the number of nuclei of the daughter amoebae produced may be equal (Figs. 26, 42) or unequal (Figs. 22, 28) or in which the daughter amoebae may be unequal in size (Fig. 27). The number of nuclei present in amoebae undergoing division of the body may vary in number from two to twenty or more. Division is therefore not associated in any way with body size, but can take place at any stage of growth of the individual. It is usual for the division of the body to take place independently of nuclear division and with all the nuclei in their resting phase; but individuals have been seen (Fig. 30) in which the body had begun to divide before the reorganization of the daughter nuclei was complete.

In working through smears from a large number of infected larvae it is very noticeable that both cytoplasmic and nuclear divisions may be rare or wholly absent amongst amoebae from some larvae, whereas, amongst amoebae from other larvae, stages in nuclear division and division of the body are frequent.

In addition to amoeboid forms of *D. mesnili*, Keilin described spherical, thin-walled cysts 8–11μ in diameter. Usually the cysts were binucleate, but he also found forms with three or four nuclei. The cytoplasm of the cysts was very much vacuolated. He also described amoeboid forms with large vacuoles in the cytoplasm, and these he considered to be intermediate between typical amoebae and cysts. Vacuolated cysts, similar to those described by Keilin, have been frequent in our material and often have occurred in masses. Binucleate forms are most common (Figs. 40, 41) as Keilin stated, but forms with three or four nuclei are also frequently seen (Figs. 36, 37). Cysts with from five to twelve nuclei have been found (Fig. 38) though they are rare. The wall of the cyst is single and very thin and the cytoplasm contains many large vacuoles. Chromatoids are absent from the cysts. There does not appear to be any reserve of glycogen. The nuclei are smaller than those usually found, at the resting phase, in the amoebae. In some cysts the nuclei are very small (Fig. 41). Amoeboid forms with vacuolated cytoplasm similar to that of the

cysts are not rare and are probably precystic forms (Fig. 39). Like the cysts these vacuolated amoebae usually contain only a few nuclei. The vacuoles in the cytoplasm of these forms are much larger than those present in the typical amoeboid stage. Cysts which were kept at room temperature (20–22° C.) for 24 hr., in serum saline solution (p. 504) in a hanging-drop preparation, did not undergo any change, and we have been unable to elucidate their further development. Amongst the hundreds of cysts which we have studied nuclear division has never been seen.

V. DISCUSSION

If the structure, and the life history in so far as we have been able to describe it, of *Dobellina mesnili* are compared with those of members of the genus *Entamoeba* it is obvious that they differ in many important characters from them. Like all the members of the genus *Entamoeba*, *Dobellina mesnili* is parasitic, but it differs from them in its mode of nutrition which is purely by osmosis and is therefore even more restricted than that of the tissue parasite *Entamoeba histolytica* which feeds by osmosis and also ingests erythrocytes and fragments of host tissue cells (Dobell & O'Connor, 1921).

The refringent granules present in such large numbers in the cytoplasm of *Dobellina mesnili* have not been described in species of *Entamoeba*, and the adhesive nature of the cytoplasm at the posterior end is not usual in species of that genus.

In nuclear structure also *Dobellina mesnili* differs from the genus *Entamoeba*. The type of nucleus associated with the Entamoebae is vesicular. It is bounded by a delicate achromatic nuclear membrane on the inside of which is deposited a layer of chromatin granules, varying in thickness according to the species, and has a small, centrally or eccentrically placed karyosome which is partly chromatic, separated from the peripheral chromatin by an area free from chromatin or containing scattered chromatin granules. The karyosome of *Dobellina mesnili* is much larger in proportion to the size of the nucleus than is the case in the genus *Entamoeba* and only a narrow achromatic area separates it from the nuclear membrane which normally is devoid of chromatin. If preparations of *Dobellina mesnili* are compared with those of species of *Entamoeba* the difference in appearance of the nucleus is most striking. During division of the nuclei of *Dobellina mesnili* the shape of the spindle, its minute size and delicacy, and the aggregation of the chromatin at the equator to form a plate, produce a picture quite different from that presented at division by the nuclei of members of the genus *Entamoeba* (e.g. *E. histolytica* or *E. aulastomi*).

The amoeboid stage of *Dobellina mesnili* may be uninucleate but more frequently it is multinucleate, whereas in the genus *Entamoeba* the trophic amoebae are uninucleate, and multinucleate forms occur only during encystation and metacystic development. This difference in the number of nuclei

present in the amoeboid stage of *Dobellina mesnili*, as compared with the trophic stages in the genus *Entamoeba*, arises from the fact that in *Dobellina* division of the nucleus is not necessarily followed by division of the body, whereas in the genus *Entamoeba* it is normal for cytoplasmic division to follow directly upon nuclear division.

The thin-walled, vacuolated cysts of *Dobellina mesnili*, devoid of chromatoids and of glycogen, are quite different in appearance from the cysts of species of *Entamoeba*. In *Dobellina mesnili* nuclear division has never been seen in the cysts whereas such divisions are a normal part of the development of the cyst in the genus *Entamoeba*.

It is therefore obvious that this parasite (*Dobellina mesnili*) differs too greatly from all species of *Entamoeba* to be included in that genus. The question then arises whether *Dobellina mesnili* belongs to any of the other genera of parasitic amoebae, which have been described. It is obvious from its structure, method of multiplication, and the multinucleate condition of the majority of individuals in the trophic stage that it bears no relationship to the genera *Endamoeba*, *Endolimax*, *Iodamoeba* and *Dientamoeba*. *Malpighiella refringens*, a small amoeboid organism, described by Minchin (1910) from the malpighian tubules of the rat flea *Ceratophyllus fasciatus*, is, like *Dobellina mesnili*, devoid of food vacuoles and nourishes itself by osmosis; but the amoeboid phase is, according to Minchin, uninucleate, and the cysts are quadrinucleate and thick-walled and thus bear no resemblance to those of *D. mesnili*. Alexeieff (1913) described from the vagina of *Hirudo medicinalis* an amoeboid organism which he included in the genus *Malpighiella*. This organism has been studied by one of us though the results are as yet unpublished. The structure of the nucleus of the amoeboid phase is very similar to that of *Dobellina mesnili* and multinucleate stages exist, but the organism differs from *D. mesnili* in that the cysts contain masses of ribbon-like chromatoids and the nuclei of the cyst resemble those of *Endolimax* rather than those of *Dobellina*.

The amoeba described by Brumpt & Lavier (1935) from the intestinal content of *Cercopithecus ruber*, and for which they created the genus *Hyalolimax*, possesses a nucleus which, at the resting stage, bears a strong resemblance to that of *Dobellina mesnili*. *Hyalolimax cercopitheci* is sometimes binucleate, but never multinucleate, and its method of division is a promitosis similar to that of *Vahlkampfia*, and quite different from the mitosis found in the dividing nucleus of *Dobellina mesnili*.

It therefore seems obvious that *D. mesnili* bears no immediate relationship to any parasitic amoeba described hitherto and the creation of a new genus for it seems justified. As we propose to name the new genus *Dobellina*, *Entamoeba mesnili* now becomes *Dobellina mesnili* and is at present the only species of this new genus.

VI. DIAGNOSIS OF THE GENUS *DOBELLINA*

Dobellina nov.gen. Amoeba measuring $3{\cdot}6 \times 3{\cdot}6$–$25 \times 15\mu$. Cytoplasm differentiated into ectoplasm and endoplasm. Pseudopodium usually single, anteriorly directed, formed of ectoplasm only. Endoplasm usually contains many refringent granules. No contractile vacuole and no food vacuoles. Amoeboid phase uninucleate or multinucleate. No differentiation in function of nuclei. Each nucleus contains a large central karyosome surrounded by a clear halo and is bounded by an achromatic nuclear membrane. Nuclei divide mitotically and simultaneously. Nuclear division is not usually followed immediately by cytoplasmic division. Division of the body may be into two, three or four daughter amoebae.

Cysts measure 8–11μ and are vacuolated and thin-walled, devoid of chromatoids and of glycogen. They usually contain two nuclei but may be multinucleate. Division of the nuclei in the cyst has not been seen. Habitat: in the space between the peritrophic membrane and the epithelium of the gut in the larvae of *Trichocera* (Diptera, Trichoceridae).

Only known species *Dobellina mesnili* (= *Entamoeba mesnili* Keilin, 1917).

VII. SUMMARY

1. A detailed morphological study has been made of the amoeba, parasitic in larvae of *Trichocera*, which was described by Keilin (1917) under the name *Entamoeba mesnili*.

2. This study shows that the parasite cannot be included in any of the existing genera of parasitic amoebae and the new genus *Dobellina* is formed for it. A diagnosis of the genus *Dobellina* is given.

3. In Cambridge *Trichocera* larvae were never found infected with *Dobellina mesnili* earlier in the winter than January and the infection rate appears to be highest (up to 92%) towards the end of January and in February. Infected larvae were never found later in the year than May.

ACKNOWLEDGEMENT. We wish to express our thanks to Dr F. W. Edwards, F.R.S., British Museum (Natural History), for kindly identifying the imagines of *Trichocera*.

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EXPLANATION OF PLATES XIII AND XIV

All figures were drawn with an Abbe camera lucida under a 1/12 in. fluorite oil-immersion lens (Leitz), with a ×20 periplanatic eyepiece. The approximate magnification of Figs. 1–28 is 3300 diameters and of Figs. 29–46 is 2640 diameters. With the exception of Figs. 43–46 the preparations were fixed with Schaudinn's solution and were stained with iron haematoxylin. Figs. 43–46 were fixed with Schaudinn's solution and were subjected to Feulgen's nucleal reaction for nucleo-protein.

PLATE XIII

Dobellina mesnili

Fig. 1. Small uninucleate amoeba.
Fig. 2. Larger uninucleate amoeba.
Fig. 3. Uninucleate amoeba with bacteria adhering to the posterior end.
Fig. 4. Binucleate amoeba with bacteria adhering to the posterior end.
Fig. 5. Binucleate amoeba showing fine strands radiating from the karyosome to the nuclear membrane.
Fig. 6. Amoeba with five small nuclei and a hyaline lobopod.
Fig. 7. Amoeba with four morula-like nuclei.
Fig. 8. Amoeba with three morula-like nuclei and bacteria adhering to the posterior end.
Fig. 9. Amoeba with many small nuclei and large, hyaline lobopod.
Fig. 10. Amoeba with eight nuclei.
Fig. 11. Large amoeba with twenty-one nuclei.
Fig. 12. Amoeba with nine nuclei. The membrane of each nucleus is siderophilic.
Fig. 13. Amoeba with six nuclei. Fine strands joining the karyosome to the nuclear membrane are visible in some of these nuclei.
Fig. 14. Quadrinucleate amoeba dividing to form two binucleate amoebae.
Fig. 15. Amoeba with six large nuclei dividing to form one large five-nucleate amoeba and one small uninucleate amoeba.
Fig. 16. Amoeba with eight nuclei dividing to form two quadrinucleate amoebae.
Fig. 17. Amoeba with seven nuclei dividing to form one trinucleate amoeba and one quadrinucleate amoeba.
Fig. 18. Amoeba with five nuclei dividing to form one binucleate amoeba and one trinucleate amoeba.
Fig. 19. Amoeba with seven nuclei dividing to form two amoebae, one having two and the other five nuclei.
Fig. 20. Amoeba with eleven nuclei dividing to form a large nine-nucleate amoeba and a small amoeba with two nuclei.
Fig. 21. Amoeba with six nuclei dividing to form two trinucleate amoebae.
Fig. 22. Amoeba with seventeen nuclei dividing into three to form two six-nucleate amoebae and one five-nucleate amoeba.
Fig. 23. Amoeba with eight nuclei dividing to form one trinucleate amoeba and one five-nucleate amoeba.

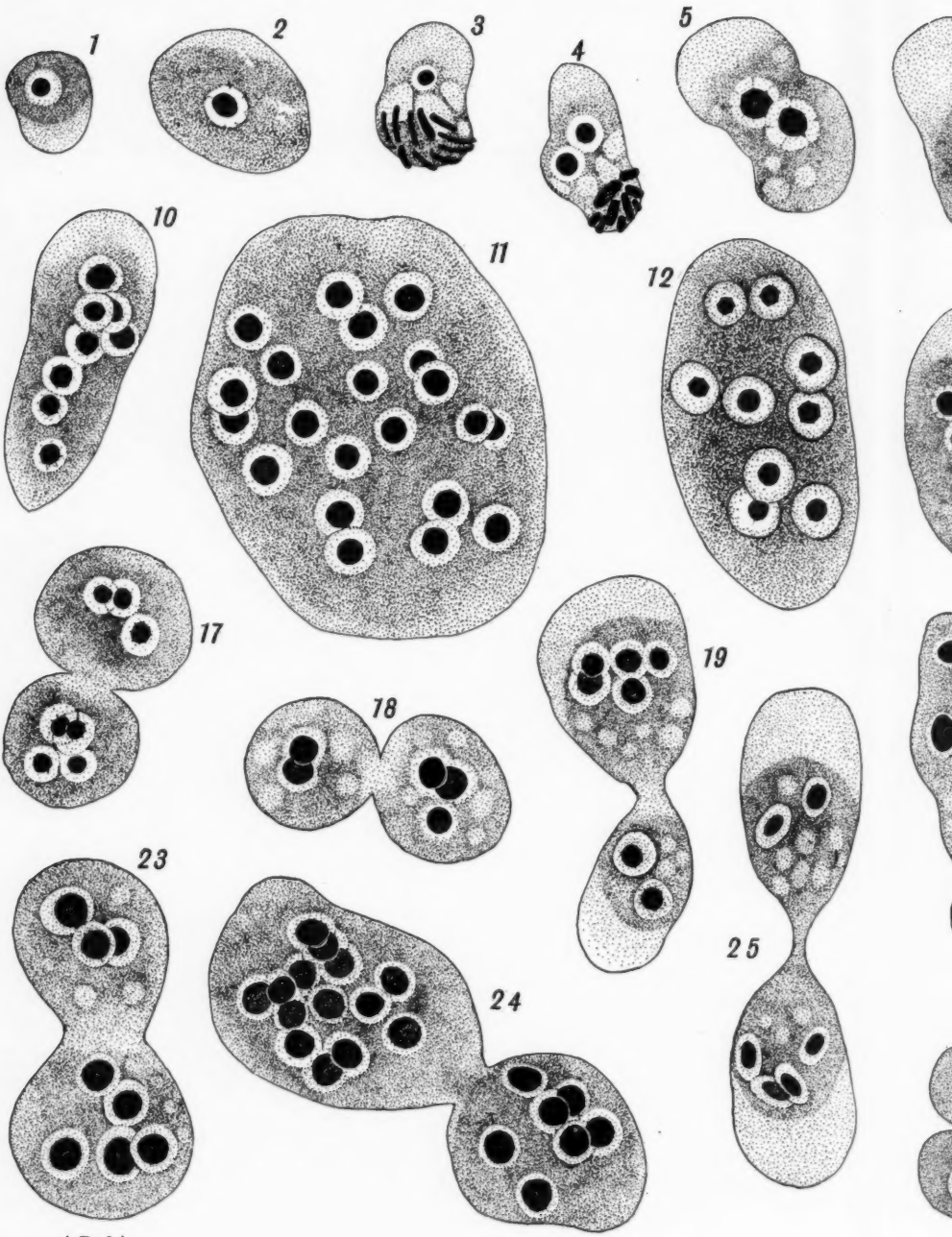

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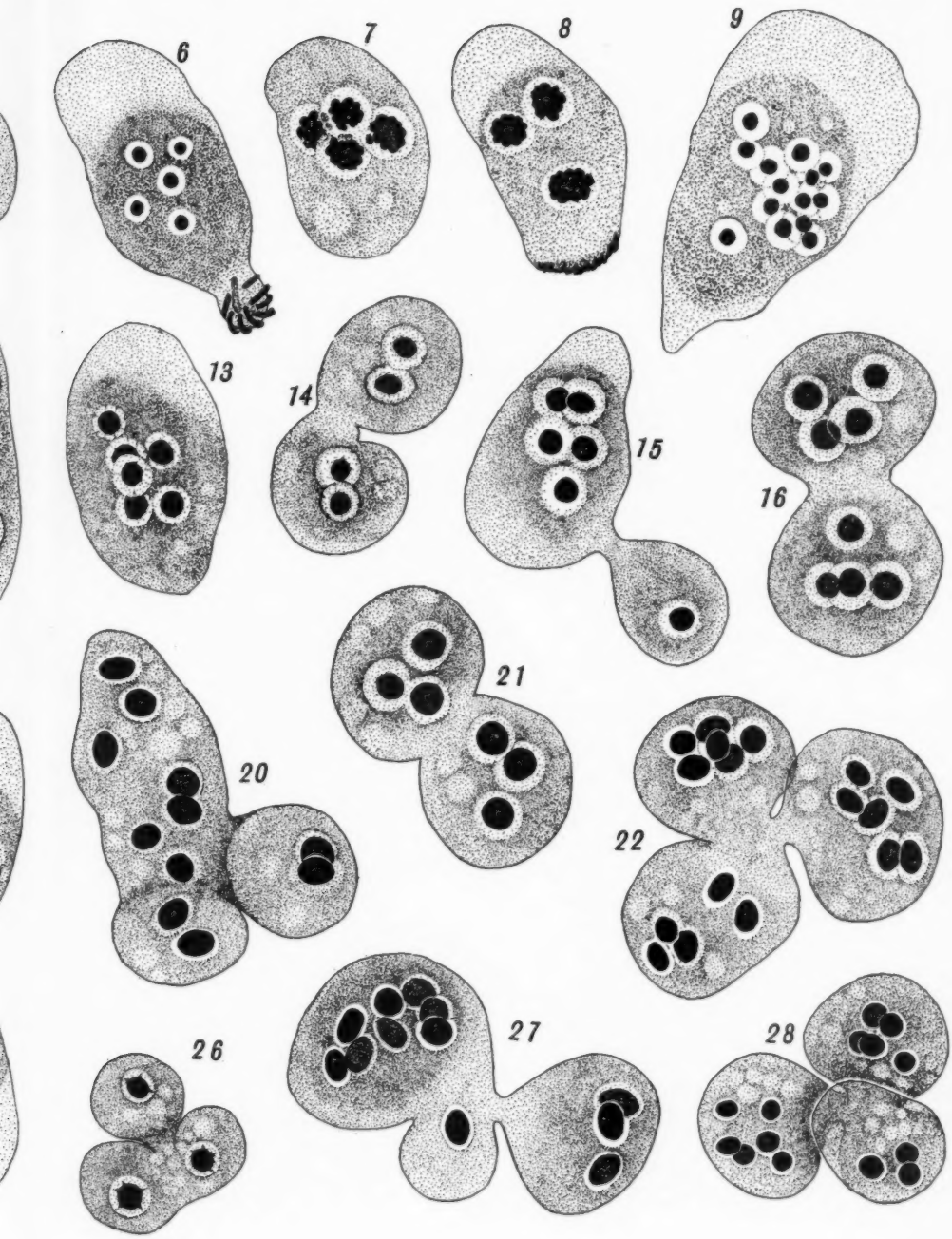
PLATE XIII



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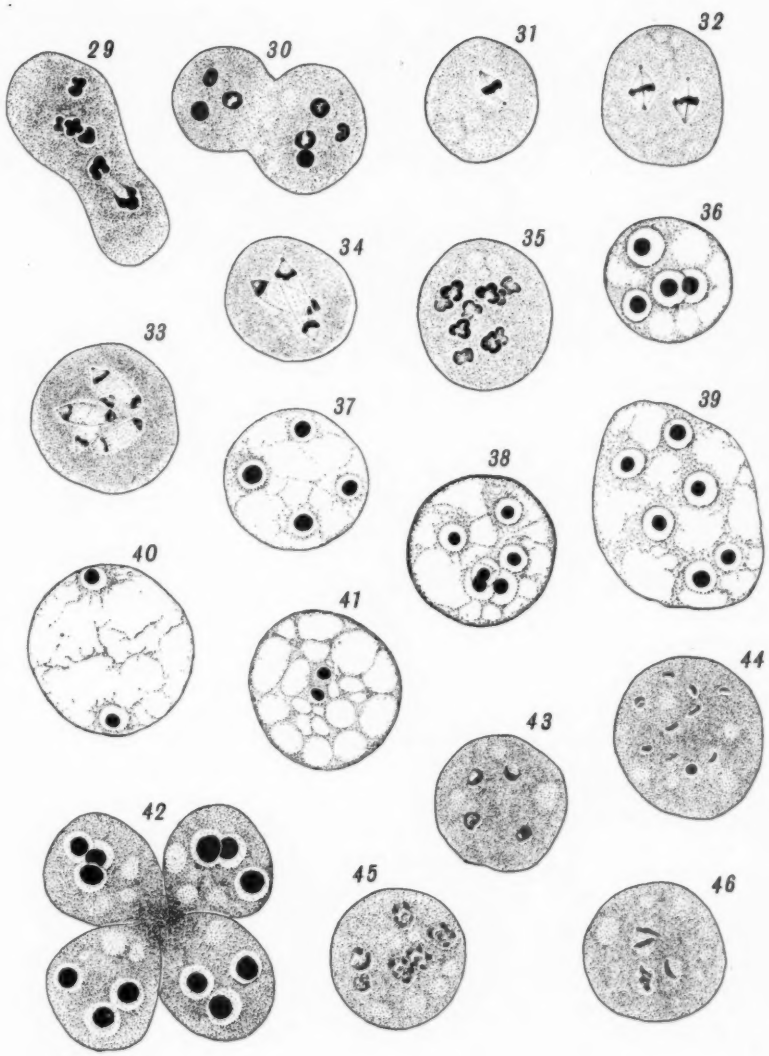

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Fig. 24. Amoeba with twenty-one nuclei dividing to form a large fourteen-nucleate amoeba and a smaller seven-nucleate amoeba.

Fig. 25. Amoeba with six nuclei dividing to form a binucleate amoeba and a quadrinucleate amoeba.

Fig. 26. A trinucleate amoeba dividing to form three uninucleate amoebae.

Fig. 27. Amoeba with twelve nuclei dividing to form one large eight-nucleate amoeba, a smaller trinucleate amoeba and a small uninucleate amoeba.

Fig. 28. Amoeba with fourteen nuclei dividing to form one six-nucleate amoeba, one five-nucleate amoeba, and one trinucleate amoeba.

PLATE XIV

Fig. 29. A trinucleate amoeba in which the nuclei are just completing their division to form six daughter nuclei.

Fig. 30. Amoeba with one nucleus at the resting stage and six daughter nuclei in different stages of reconstruction after division.

Fig. 31. A uninucleate amoeba in which the nucleus is dividing. A spindle with equatorial plate, centrosomes and centrodesmose is present.

Fig. 32. A binucleate amoeba in which both nuclei are dividing simultaneously.

Fig. 33. A quadrinucleate amoeba in which the nuclei are dividing simultaneously. The chromatin of each nucleus is in two plates which are moving towards opposite poles of the spindles.

Fig. 34. A binucleate amoeba in which the dividing nuclei are at the same stage as those in Fig. 33.

Fig. 35. An amoeba containing ten daughter nuclei which are undergoing reconstruction after division.

Fig. 36. A cyst with vacuolated cytoplasm and four nuclei.

Fig. 37. A four-nucleate cyst with cytoplasm greatly vacuolated.

Fig. 38. A cyst containing six nuclei.

Fig. 39. An amoeba, with vacuolated cytoplasm, containing six nuclei.

Fig. 40. A binucleate cyst.

Fig. 41. A binucleate cyst with very small nuclei.

Fig. 42. A twelve-nucleate amoeba undergoing division to form four trinucleate amoebae.

Fig. 43. An amoeba with four daughter nuclei undergoing reconstruction after division (Feulgen).

Fig. 44. An amoeba with ten daughter nuclei, some undergoing reconstruction whereas others are still at the late telophase (Feulgen).

Fig. 45. An amoeba with six nuclei. The chromatin is arranged mostly on the surface of the karyosome (Feulgen).

Fig. 46. An amoeba with four nuclei undergoing division. The chromatin is arranged on the equatorial plate (Feulgen).

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